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Superorganismality and caste differentiation as points of no return: how the major evolutionary transitions were lost in translation

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ABSTRACT

More than a century ago, William Morton Wheeler proposed that social insect colonies can be regarded as superorganisms when they have morphologically differentiated reproductive and nursing castes that are analogous to the metazoan germ-line and soma. Following the rise of sociobiology in the 1970s, Wheeler's insights were largely neglected, and we were left with multiple new superorganism concepts that are mutually inconsistent and uninformative on how superorganismality originated. These difficulties can be traced to the broadened sociobiological concept of eusociality, which denies that physical queen–worker caste differentiation is a universal hallmark of superorganismal colonies. Unlike early evolutionary naturalists and geneticists such as Weismann, Huxley, Fisher and Haldane, who set out to explain the acquisition of an unmated worker caste, the goal of sociobiology was to understand the evolution of eusociality, a broad-brush convenience category that covers most forms of cooperative breeding. By lumping a diverse spectrum of social systems into a single category, and drawing attention away from the evolution of distinct quantifiable traits, the sociobiological tradition has impeded straightforward connections between inclusive fitness theory and the major evolutionary transitions paradigm for understanding irreversible shifts to higher organizational complexity. We evaluate the history by which these inconsistencies accumulated, develop a common-cause approach for understanding the origins of all major transitions in eukaryote hierarchical complexity, and use Hamilton's rule to argue that they are directly comparable. We show that only Wheeler's original definition of superorganismality can be unambiguously linked to irreversible evolutionary transitions from context-dependent reproductive altruism to unconditional differentiation of permanently unmated castes in the ants, corbiculate bees, vespine wasps and higher termites. We argue that strictly monogamous parents were a necessary, albeit not sufficient condition for all transitions to superorganismality, analogous to single-zygote bottlenecks being a necessary but not sufficient condition for the convergent origins of complex soma across multicellular eukaryotes. We infer that conflict reduction was not a necessary condition for the origin of any of these major transitions, and conclude that controversies over the status of inclusive fitness theory primarily emanate from the arbitrarily defined sociobiological concepts of superorganismality and eusociality, not from the theory itself.

Key words: superorganism, eusociality, major evolutionary transitions, sociobiology, inclusive fitness theory, monogamy hypothesis, single-cell bottleneck.

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To be useful, the superorganism metaphor must be consistent. It should illuminate aspects of social insect biology hitherto overlooked and provide explanations based on organisms that are useful for understanding features of the superorganism. (Page & Mitchell, 1993)

[T]here is something appealing about 'eusocial' that kept expanding its horizons, while reducing its precision. I see it used popularly everywhere as jargon, by now meaning no more than simply 'social.' (Batra, 1995)

I. INTRODUCTION AND AIMS

Are eusocial colonies superorganisms? Since the 1980s, an increasing number of biologists have argued in favour of this idea. In fact, talk of superorganisms has become so commonplace that their existence is taken for granted (e.g. Lumsden, 1982; Seeley, 1989; Moritz & Southwick, 1992; Heinze, Hölldobler & Peeters, 1994; Moritz & Fuchs, 1998; Amdam & Seehuus, 2006; Detrain & Deneubourg, 2006; Tautz, 2008; Hölldobler & Wilson, 2009; Alaux, Maisonnasse & Le Conte, 2010; Gillooly, Hou & Kaspari, 2010; Johnson & Linksvayer, 2010). This lack of scrutiny matters little when emphasizing that social insects need to be studied both from the level of the colony and the animals that compose them. However, starting with Wheeler (1911), superorganism claims have also been used to convey the idea that some insect colonies represent a distinct level of organization above metazoan multicellularity. Formulated this way, superorganismality becomes shorthand for a macro-evolutionary hypothesis that such colonies may represent an entirely distinct type of life. Reaching superorganism status then becomes analogous to other major transitions, such as the convergent evolution of obligate multicellularity, as in animals, plants, some fungi, and some algae (Grosberg & Strathmann, 2007; Fisher, Cornwallis & West, 2013; Lang & Rensing, 2015). The claim that colonies are superorganisms is a strong assertion, so there should be no ambiguity about which social organisms have and have not made this transition. However, incoherent definitions and casual use of terminology have made it difficult to make such decisions and to identify the origins of major transitions.

This lack of clarity has hindered the development of a unified account of social evolution across the levels of biological organization.

All superorganisms identified by Wheeler (1911) are presently considered to be eusocial, which is commonly taken to imply that they have: (i) cooperative brood care, (ii) reproductive division of labour, and (iii) overlap of adult generations. This three-part eusociality definition has been widely used for over four decades, but few have noticed that in setting it out in the first pages of *The Insect Societies*, Wilson (1971) broke with earlier zoological classifications of social organization. The term eusociality was originally formulated to describe only ground-nesting halictid bees whose nest foundresses recruit some daughters as helpers. It did not refer to social insects in general, and particularly not to those with physically differentiated castes (Batra, 1966a). The broadened definition (Wilson, 1971, 1975, 1985) made it impossible for lineages with permanent castes to be considered fundamentally more advanced than, and hence distinct from, those with temporal and plastic helper phenotypes. This problem was first identified when Peeters & Crozier (1988, p. 284) noted that caste, as redefined by Wilson (1985), had simply become 'a set of colony members, smaller than the total colony population, that specialize on particular tasks for prolonged periods of time'. The new eusociality definition contrasted with the explicit acknowledgement of the evolutionary importance of physical queen–worker caste differentiation by Darwin (1859), Weismann (1893) and Wheeler (1911, 1928a), as well as modern (neo-Darwinian) synthesis architects such as Fisher (1930) and Huxley (1930). It is thus opportune to ask why the field did not continue using the term eusociality for monomorphic cooperative breeding in matrifilial nests permanent enough to accommodate more than a single generation (Batra, 1966a), and superorganismality (Wheeler, 1911) for colonies with physically polymorphic queen and worker castes. New superorganism concepts were developed in the 1980s, but without reference to the scientific advances that allegedly undermined the original version of Wheeler (1911) which treated obligatorily co-dependent

germ–soma specialization of castes as a crucial evolutionary innovation.

Because discussions of eusociality and superorganismality often make reference to major evolutionary transitions, it is important to be explicit about what these are. We follow Maynard Smith & Szathmáry (1995) in considering them to be evolutionary changes in hierarchical complexity that involve both a loss of independent breeding and higher-level adaptations to more inclusive levels of organization. However, we maintain that, to be major, such transitions must also be defined as evolutionarily irreversible. This occurs when obligate differentiation between germ and soma functions can be unambiguously identified, and switches to higher levels of heritability and ontogeny are completed. Evolutionary changes of this type require fundamentally new developmental pathways to become established and go to fixation, occasionally allowing secondary (usually parasitic) reductions but no reversals to ancestral free-living states. With rare exceptions (West *et al.*, 2015), the point that major transitions need to be phylogenetically irreversible has been at best tentatively admitted because of no evidence to the contrary (e.g. Szathmáry & Maynard Smith, 1995; McShea, 2001; Bourke, 2011a). The necessity of making irreversibility an explicit, testable assumption of the major evolutionary transitions paradigm is obvious when such transitions also create fundamentally novel and permanent assemblies of what Cosmides & Tooby (1981) coined ‘co-replicons’. These are formerly self-replicating units that retain distinct reproductive interests even after reproducing with other co-replicons has become mandatory due to irreversible morphological specialization. The paradigmatic example of a partnership between co-replicons is the origin of the first eukaryote cell, defined as an egalitarian major transition by Queller (2000).

For the social insects, transitions were fraternal rather than egalitarian, as they concern the same gene pool (Queller, 2000). Such transitions have recently been re-associated with point of no return origins of physically differentiated castes (Wilson & Hölldobler, 2005). This allowed reference (Wilson & Wilson, 2007) to the general major transitions framework (Maynard Smith & Szathmáry, 1995), but this acknowledgement of the evolutionary significance of morphological castes stands in direct opposition to the sociobiology-inspired conception of eusociality that all but erased the importance of distinct queen–worker polymorphism some four decades ago (Wilson, 1975, 1985; Sherman *et al.*, 1995).

Because multiple modern concepts of superorganismality coexist in the literature with Wheeler’s (1911) original version, they cannot all correctly identify the points of no return that demarcate the origins of major evolutionary transitions. Resolving this ambiguity is important because our understanding of the evolutionary forces that have shaped biological complexity should not be based on arbitrary constructs, but on rigorous procedures that first parse social phenotypes into biologically meaningful groups defined by the presence or absence of evolutionarily important traits, and then unambiguously assess the point of no return clicks of

the evolutionary ratchet that constitute major transitions. As we summarized above, the modern literature on superorganismality, eusociality, and major transitions has fundamental ambiguities that preclude a unified view of the evolutionary history of eukaryotic hierarchical complexity which the architects of the modern synthesis had no problem seeing. Re-reading their contributions is reminiscent of exploring an intellectual fossil record, because their inferences about social evolution were almost never cited after the 1950s. Yet, they rarely strike the modern reader as being mistaken because of data that we have and they lacked, so there must be some other reason these works were lost in the second half of the 20th century, and this deserves to be made explicit.

Our present review confronts 40 years of sociobiology heritage with the need to be coherent about eusociality, organismality, superorganismality and irreversibility, as demanded by the first epigraph (Page & Mitchell, 1993), and in sharp contrast to what has actually happened, according to the second epigraph (Batra, 1995). To do so, we review the origin and later modifications of the superorganism concept to show that all later versions are imprecise compared to Wheeler’s (1911) original, and unsuitable for capturing the origins of major transitions, a focus that has been surprisingly neglected (but see Bourke, 2011a; Clarke, 2014). We then proceed to outline that the parallels between the points of no return to complex multicellular organismality and colonial superorganismality are even more striking than Wheeler (1911) imagined, and that all major hierarchical transitions since the last eukaryote common ancestor (LECA) appear to hinge on (super)organismal foundation principles that always create maximal relatedness among adhering cell copies or colonial siblings – a predicted and confirmed pattern that forges coherent general connections with inclusive fitness theory (Hughes *et al.*, 2008; Fisher *et al.*, 2013). Finally, we discuss why intra-(super)organism conflict reduction is relevant for secondary elaborations but not for major transition origins, and how the ‘just so’ definitions of sociobiology have fuelled fruitless debates that would probably not have arisen if the earlier, more-coherent definitions of eusociality and superorganismality had been retained. We conclude that hypotheses which purport to provide insight into the evolution of Wilson’s unspecified eusociality have not been, and cannot be, validated because such an artificial behavioural category does not respond to selection – only distinct biological traits such as the expression of reproductive altruism, and the proximate mechanisms that give rise to caste phenotypes do.

A brief historical overview of the five key concepts addressed in these introductory paragraphs is given in Table 1 to provide context for our more comprehensive review of the superorganism in the sections that follow. To facilitate understanding of the shifting ways in which key authors have conceived and handled the concepts of (eu)sociality and (super)organismality over a period of almost 125 years, we have also compiled a list of more than 50 numbered quotations that we refer to with qE (eusociality), qS (superorganismality) and qN (non-social insects) prefixes throughout the text (Table 2).

Table 1. The five concepts analysed in this review

<p>Superorganism: originally a sociological term introduced by Spencer (1885) to argue that human societies have organism-like properties. The term remained a facile unscientific concept until Wheeler (1911) referred to insect colonies in which all members belonged to one of several morphologically distinct castes as ‘organismal’, and later called them ‘superorganismal’, to emphasize that they represent a distinct domain of social evolution beyond metazoan multicellularity. Subsequent versions of the superorganism lost connection to physical caste differentiation, which reinstated Spencerian connotations of unspecified harmony at all biological scales (e.g. Emerson, 1952). This purportedly led to the demise of the superorganism concept in the 1950–1960s. Different kinds of superorganism concepts arose in the late 1980s, but without clear definitions (Seeley, 1989; Wilson & Sober, 1989). In this review we categorize these new concepts as <i>sensu lato</i> and <i>sensu stricto</i> superorganismality capturing, respectively, the idea that either all or only the most evolutionarily derived social insect colonies are assumed to be superorganismal (Hölldobler & Wilson, 2009).</p>
<p>Eusociality: a term coined by Batra (1966a). It originally referred exclusively to subsocial (mother–offspring) associations in ground-nesting halictid bees, i.e. to very small insect families lacking any sort of morphological division of labour. Later, the term was generalized to characterize most forms of social breeding (Michener, 1969; Wilson, 1971, 1975, 1985, 2012, 2014; Batra, 1995). It is generally unknown that Huxley (1930, p. 10) coined the term ‘true social, or colony, grade’ in 1930 to refer to the same type of social organization identified by the Batra (1966a) definition of eusociality. He received no credit for this, which we redress herein.</p>
<p>Major transitions in evolution: a concept developed by Maynard Smith & Szathmáry (1995) to highlight the fact that life has increased in hierarchical complexity over time, starting with molecular replicators that produced chromosomes and prokaryote cells, which in turn gave rise to the first eukaryote ancestor, various independent forms of obligate multicellularity and finally colony-life with physically differentiated queen and worker castes. The concept was further elaborated by Queller (2000), who noted that transitions could be either fraternal or egalitarian. Before Maynard Smith & Szathmáry (1995), Buss (1987) and Bonner (1988) had attempted independent analyses of the advancement of biological complexity, and during the first decades of the 20th century, Huxley (1912) developed the contours of a similar framework, but this contribution appears to have been ignored by later authors.</p>
<p>Sociobiology: a comparative narrative developed by Wilson (1971, 1975) (see also Oster & Wilson, 1978) and defined as ‘the systematic study of the biological basis of all forms of social behavior’ that is ‘based to a substantial degree on population biology, including the ecology and genetics of populations, and thereby stresses not only behavior but also the demography and structure of whole societies.’ (Wilson, 1983, p. 552). The approach was greeted with controversy, but became well known among professional academics and the lay-public, despite contributing little to the development of new testable evolutionary hypotheses, or the further advancement of social evolution theory from first principles. This contrasts with the field of behavioural and evolutionary ecology that developed simultaneously (Krebs & Davies, 1978, 1984, 1991, 1997; Trivers, 1985; Cockburn, 1991; Dawkins, 1999), which is often mentioned jointly with sociobiology.</p>
<p>Inclusive fitness: a first-principle theory developed by Hamilton (1963, 1964a,b, 1972) for explaining the evolution and maintenance of cooperation, altruism, spite and selfishness (West, Griffin & Gardner, 2007). The early insights of Hamilton were used approvingly by Williams (1966), who offered the first synthetic treatment of biological adaptation based on universal ‘gene’s eye’ arguments after Darwinism and Mendelism had been reconciled (Cronin, 1991; Boomsma, 2016). Inclusive fitness theory allows for the formulation of many testable hypotheses about social adaptations, based on maximizing the representation of genes coding for relevant social behaviours in future generations via direct reproduction, and/or indirect reproduction through relatives. The theory became fully mature after key contributions by Trivers (1974), Trivers & Hare (1976), Hamilton (1975), Cosmides & Tooby (1981), and Grafen (1984) and more recently, Queller (1996), Frank (1998) and Grafen (2014). Inclusive fitness theory and its universal gene-copy currency was made accessible to a wide readership by Dawkins (1976) around the same time that sociobiology (Wilson, 1975) was introduced and debated. The actual process by which the indirect component of inclusive fitness is maximized is known as kin selection (Maynard Smith, 1964).</p>

II. HISTORY

(1) The early history of the superorganism: how Wheeler’s concept became neglected

The first misconception we intend to address is the notion that Wheeler’s (1911) superorganism concept was initially embraced by other social insect researchers, fell out of favour after 1950 (Wilson, 1967, 1971; Lumsden, 1982; Wilson & Michener, 1982; Hölldobler & Wilson, 1990; Page, 2013), and was resurrected in the 1980s. Our review of the early 20th-century literature appears to support a different reading. Wheeler began drawing comparisons between ant colonies and metazoans (Wheeler, 1902) (Table 2, qS2) a decade before he explicitly stated that insect colonies are organisms when they have permanent, morphologically differentiated castes (Wheeler, 1910, 1911) (Table 2, qS3 and qS4). In doing this, he stood on the shoulders of giants such as August Weismann (Table 2,

qE1, qE2 and qS1), and later had the support of R.A. Fisher and Julian S. Huxley (Table 2, qE4, qS5 and qS8), two co-founders of the modern (neo-Darwinian) synthesis. As summarized by Mitchell (1995), Wheeler noted that (super)organismal colonies behave as ‘unitary wholes’, have differentiated germ (reproductive) and soma (worker) lines, and develop both ontogenetically and phylogenetically over time (Table 2, qS2–4, qS6 and qS7). His position was not simply that colonies resemble organisms, or that treating them as such can be a useful idealization. He believed that colonies are organisms in the full sense of the word (Table 2, qS4). In later works he began to use the now familiar superorganism terminology (Wheeler, 1928a), but his underlying views remained unchanged (Table 2, qS6 and qS7). The assumption that superorganismality constitutes a domain of social evolution that is analogous to, but distinctly beyond/above (the meaning of the Latin prefix ‘super’) animal zygote-derived multicellularity, was always central to Wheeler’s reasoning (Table 2, qS2–4, qS6 and qS7).

Table 2. A chronological sample of relevant quotes on (eu)sociality (qE1–qE23) and insect colony superorganismality (qS1–qS25) found in the literature since the 1890s, with indications of primary taxonomic affiliation and generality, supplemented with representative quotes of extensions of the superorganism concept outside the realm of social insects (qN1–qN7) that have clouded transparency

Eusociality, including earlier and later social classification schemes

- qE1.** *Social*: (insects; Weismann, 1893, p. 325) '[I]n the case of the ants, every little improvement in the workers proceeds from the variation of a determinant of the germ-plasm that was contained in the germ-cells of the parents.'
- qE2.** *Social*: (insects; Weismann, 1893, p. 327) 'Obviously the workers must be more rapidly improved when all in a hive are the progeny of one queen – i.e., if they are all alike or almost alike.'
- qE3.** *Social*: (insects; Wheeler, 1928*b*, p. 13) '[P]rogeny are not only protected and fed by the mother, but eventually co-operate with her in rearing additional broods of young, so that parent and offspring live together in an annual or perennial society.'
- qE4.** *Social*: (insects; Huxley, 1930, p. 10) 'Three main grades of social habit may be distinguished. In the lowest there is some sort of a family life, either the mother or both parents living with and helping the developing young. This may be called the sub-social, or family, grade. The second is the true social, or colonial, grade, in which the young, when fully grown, stay with their parents and co-operate with them in building the nest and caring for further broods of young. The highest grade is that of the caste-society, in which some of the young are transformed into unsexed "neuters", who take off the shoulders of the fertile caste all the duties of the colony, save only that of reproduction.'
- qE5.** *Social*: (insects; Haldane, 1932, p. 120) 'In the case of social insects there is no limit to the devotion and self-sacrifice which may be of biological advantage in a neuter. In a beehive the workers and young queens are samples of the same set of genotypes, so any form of behaviour in the former (however suicidal it may be) which is of advantage to the hive will promote the survival of the latter, and thus tend to spread through the species. The only bar to such a spread is the possibility that the genes in question may induce unduly altruistic behaviour in the queens. Genes causing such behaviour would tend to be eliminated.'
- qE6.** *Social*: (insects; Sturtevant, 1938, p. 74) 'In terms of natural selection, a "favorable" character is of course to be taken as meaning a character that leads to the production of more descendants. The sterile castes of the insects named [termites, ants, and many bees and wasps] have, therefore, developed a character that is unfavorable by definition. . . . In order that the colony be the unit in terms of natural selection, and that the existence of the sterile caste offer no difficulties to the advocates of pure selection, it is necessary that each colony have a single fertile queen and that the sterile individuals all be closely related to the queen (presumably her offspring).'
- qE7.** *Social*: (insects; Emerson, 1939, p. 198) 'We may consider degenerative loss of the sterile castes as a parallel to the loss of many somatic tissues in the parasitic crustacean, *Sacculina*.'
- qE8.** *Eusocial*: (halictid bees; Batra, 1966*a*, p. 375) '[E]usocial behavior, in which the nest-founding parent survives to cooperate with a group of her mature daughters, with division of labor'
- qE9.** *Semisocial*: (bees; Michener, 1969, p. 304) 'Division of labor, with both egg layers and workerlike individuals among adult females. . . . All the females are of the same generation, unlike those in the matrifilial colonies of eusocial forms.'
- qE10.** *Primitively eusocial*: (bees; Michener, 1969, p. 305) 'Among primitively social bees, female castes are externally indistinguishable in structure except for allometric macrocephaly (often intergrading) of some queens.'
- qE11.** *Highly eusocial*: (bees; Michener, 1969, p. 306) 'The highly or complexly social bees have female castes strikingly different from one another, not only behaviorally, physiologically, and usually in size, but also in external structure.'
- qE12.** *Eusocial*: (ants and other insects; Wilson, 1971, p. 4) 'The "truly" social insects, or eusocial insects as they are sometimes more technically labeled, include ants, all termites, and the more highly organized bees and wasps. These insects can be distinguished as a group by their common possession of three traits: individuals of the same species cooperate in caring for the young; there is a reproductive division of labor, with more or less sterile individuals working on behalf of fecund individuals; and there is an overlap of at least two generations in life stages capable of contributing to colony labor, so that offspring assist parents during some period of their life.'
- qE13.** *Eusocial*: (insects; Wilson, 1975, pp. 125 and 299) 'The very definition of higher sociality ("eusociality") in termites, ants, bees, and wasps entails the existence of sterile castes whose basic functions are to increase the oviposition rate of the queen, ordinarily their mother, and to rear the queen's offspring, ordinarily their brothers and sisters. . . . In social insects a caste is any set of individuals of a particular morphological type, or age group, or both, that performs specialized labor in the colony. It is often more narrowly defined as any set of individuals that are both morphologically distinct and specialized in behavior.'
- qE14.** *Eusocial*: (bees; Batra, 1977, p. 291) 'The single nest-founding female *eusocial* bee at first performs all duties; then when the daughters mature, they remain in their natal nest and serve as workers, and the foundress remains as the egg laying queen (Batra, 1966*a*). . . . *Hypersocial* here is coined to refer to the very different social arrangement of honey bees and stingless bees in which the queen is structurally and behaviourally specialized only for egg laying; she cannot begin a new nest without the help of a swarm of workers (considered as eusocial by Wilson, 1971; Michener, 1974 and many others, but not by Batra, 1966*b* . . . who first defined and used the word[]).'
-

Table 2. Continued

- qE15. *Eusocial*:** (animals; Wilson, 1985, pp. 309–310) ‘A caste is a set of colony members, smaller than the total colony population, that specialize on particular tasks for prolonged periods of time. Ordinarily, and perhaps in the social insects invariably, the set is distinguished by some kind of additional marker – a larger size, some other kind of anatomical feature, a different age, or even some less apparent physiological trait. . . . The linkage between castes and roles is close, and in the case of the more complex forms of morphological and behavioral variation, it is sometimes necessary to employ roles to distinguish castes.’
- qE16. *Eusociality continuum*:** (animals; Sherman *et al.*, 1995, p. 102) ‘Cooperative breeding and eusociality are not discrete phenomena, but rather form a continuum of fundamentally similar social systems whose main differences lie in the distribution of lifetime reproductive success among group members.’
- qE17. *Eusocial*:** (animals; Crespi & Yanega, 1995, p. 109) ‘Our criterion for eusociality is the presence of castes, which are groups of individuals that become irreversibly behaviorally distinct at some point prior to reproductive maturity. Eusocial societies are characterized by two traits: (i) helping by individuals of the less-reproductive caste, and (ii) either behavioral totipotency of only the more reproductive caste (facultative eusociality) or totipotency of neither caste (obligate eusociality). We define “cooperative breeding” as alloparental care without castes.’
- qE18. *Eusocial*:** (insects; Maynard Smith & Szathmáry, 1995, p. 268) ‘By definition, all eusocial insects show a division of labour between reproductive and housekeeping/foraging roles. In many, there is a division of labour between workers as well. The simplest type of specialization is “age polyethism”: workers of different ages perform different tasks.’
- qE19. *Eusocial*:** (insects; Batra, 1995, p. 2) ‘Thus, in 1966, I coined “eusocial”, meaning “truly social” as a simple, euphonious term to replace “primitively social”. . . . Unfortunately, I did not coin a comparable word for honey bee societies at that time . . . I did believe (and still do) that eusocial bees (and other eusocial insects such as most ants and some social wasps) actually have a superior type of queen. . . . “[E]usocial” took on a lively life of its own, creeping into review articles, then into textbooks, where it was used to describe honey bee societies (as “highly eusocial”), which defeated the purpose of its coinage.’
- qE20. *Eusociality continuum*:** (animals; Beekman *et al.*, 2006, p. 623) ‘[T]he most important shortcoming of the eusociality continuum is that a society with a single reproductive individual can result from 2 dramatically different processes: behavioral regulation or morphological specialization.’
- qE21. *Facultatively eusocial breeding*:** (animals; Boomsma, 2013, p. 3) ‘A cooperative breeding system where reproductive and helping roles are lifelong determined for a substantial fraction of the colony membership, but where a subset of offspring retains reproductive totipotency in spite of being part of a helper cohort, so they may later inherit the nest as dominant breeder or disperse to become dominant elsewhere. Caste roles are mostly behavioural and characterized by minor and overlapping distributions of body size and matedness, but some lifelong subordinates may belong to a physically distinct soldier caste. When a soldier caste is absent, there is no sharp distinction between advanced cooperative and facultatively eusocial breeding, as both combine obligate colony life with the retention of reproductive totipotency for some fraction of the subordinates.’
- qE22. *Obligatorily eusocial breeding*:** (insects; Boomsma, 2013, p. 3) ‘A breeding system in which all individuals are either designated breeders or unmated workers/soldiers for life, and where castes are always physically distinct and differentially adapted to a specific subset of social tasks so that colony growth and reproduction always require the complementary efforts of all castes. This implies that no caste has retained reproductive totipotency. The evolution of a specialized worker caste of unmated individuals is the ultimate defining character of obligate eusociality, no matter whether a worker caste evolves after (termites) or before (Hymenoptera) soldiers.’
- qE23. *Eusocial*:** (animals; Wilson, 2014, p. 19) ‘Using comparative studies of thousands of animal species, from insects to mammals, we’ve concluded that the most complex societies have arisen through eusociality – meaning, roughly, the “true” social condition.’
- Superorganismality: highlighting variation in precision**
- qS1. *(Super)organismality*:** (ants, insects; Weismann, 1893, pp. 326–327) ‘[I]n the case of the ant colony, or rather state, the barren individuals or organs are metamorphosed only by selection of the germ-plasm from which the whole state proceeds. In respect of selection the whole state behaves as a single animal; the state is selected, not the single individuals; and the various forms behave exactly like the parts of one individual in the course of ordinary selection.’
- qS2. *(Super)organismality*:** (ants, insects; Wheeler, 1902, p. 769) ‘If we look upon the ant-colony as a complex of more or less heterogeneous individuals, comparable to the Metazoan body, which is also a complex of units, the more or less differentiated cells, we may say that the sexual individuals of the ant colony develop only under favorable trophic conditions, just as the sexual organs of the Metazoan mature only under similar conditions.’
- qS3. *(Super)organismality*:** (ants, insects; Wheeler, 1910, p. 7) ‘As in the case of the individual animal, no further purpose of the colony can be detected than that of maintaining itself in the face of a constantly changing environment till it is able to reproduce other colonies of a like constitution. The queen mother of the ant colony displays the generalized potentialities of all the individuals, just as the Metazoan egg contains *in potentia* all the other cells of the body. And, continuing the analogy, we may say that since the different castes of the ant colony are morphologically specialized for the performance of different functions, they are truly comparable with the differentiated tissues of the Metazoan body.’
- qS4. *(Super)organismality*:** (insects; Wheeler, 1911, p. 310) ‘[P]ermit me to present the evidence for the contention that the animal colony is a true organism and not merely the analogue of the person.’

Table 2. Continued

- qS5.** *(Super)organismality*: (insects; Huxley, 1912, p. 142) ‘The communities of ants and bees are undoubted individuals. Wheeler in a recent paper [Wheeler (1911)] has abundantly justified this view from a somewhat different standpoint. Here I can only say that if the ideas and definitions put forward in Chap. I are accepted, their individuality is beyond dispute. In spite of space, I cannot refrain from giving one example of the lengths to which internal differentiation of parts can go in such apparently loose-connected wholes. In several species of ants there are special workers whose duty it is to imbibe honey till their fair round bellies are drum-tight, then to suspend themselves, a row of living jars, from the roof, and there to wait until their store is needed by the colony and they are taken down and tapped for general consumption.’
- qS6.** *Superorganismality*: (insects; Wheeler, 1928a, pp. 40–41) ‘[M]ulticellular organisms, whose integration is so exceedingly complicated and opaque that we are probably still centuries removed from any adequate understanding of their functional composition, but on the next level, that of the very loosely organized social, or superorganisms, in which the actual play of the components is open to inspection ...’
- qS7.** *Superorganismality*: (insects; Wheeler, 1928b, p. 23) ‘Another more general problem is suggested by the insect society, or colony as a whole, which as I have shown in another place (Wheeler, 1911) is so strikingly analogous to the Metazoan body regarded as a colony of cells, or indeed to any living organism as a whole, that the same very general laws must be involved.’
- qS8.** *(Super)organismality*: (insects, humans; Fisher, 1930, p. 181) ‘In this respect the insect society more resembles a single animal body than a human society, for although many tissues are capable by cell division of the replacement of damaged parts, yet the reproduction of the whole organism is confined to specialized reproductive tissue, whilst the remainder of the body with its various co-operative functions, co-operating with but taking no part in reproduction, is in this respect analogous to the body of sterile workers which constitutes the bulk of the hive.’
- qS9.** *Superorganismality*: (insects, humans; Huxley, 1930, pp. 9 and 120–121) ‘Innumerable comparisons have been made between human society and the social organization of ant, bee, or termite; theories have been advanced and morals pointed, Utopian schemes encouraged and whole theories of the State built up for man on the basis of analogy with these little insects. Almost without exception the moral has been false, the analogy misleadingly used. . . . There is thus no reason to suppose that man is destined to sterilize nurses or manual workers, to breed armoured or gas-resistant soldiers, communal parents the size of whales, or an intelligentsia all head and no body.’
- qS10.** *Superorganismality*: (termites; Emerson, 1939, pp. 193–194) ‘The colonizing flight of termites is an interesting example of the superorganismic parallel to the cyclic sexual activity of the organism . . . [A] remarkable sequence of definitive activity is certainly present which roughly parallels the orientation, movements and fertilization mechanism of the gametes of plants and animals.’
- qS11.** *Superorganismality*: (termites; Lüscher, 1953, p. 69) ‘If a termite colony is considered as a superorganism, then caste differentiation may be looked upon as an embryological problem. The differentiation of cells in an embryo is always initiated at a certain critical stage in their development; in other words, a given group of cells cannot change until it is ready. One may assume that a nymph in a termite colony similarly can be induced to differentiate only at a critical stage of readiness.’
- qS12.** *Superorganismality*: (*sensu lato*; Wilson, 1967, p. 27) ‘It is doubtful that the term, which is a panchreston of little relevance to the operational aspects of research, will be employed in the future except in a metaphorical sense.’ This is reference to Hardin (1956, p. 112) who dismissed the term protoplasm, writing: ‘At best, the word [which he describes as a “panchreston”] has functioned only as window dressing; at worst, it has probably impeded scientific progress.’
- qS13.** *Superorganismality*: (*sensu lato*; Oster & Wilson, 1978, pp. 21–22) ‘Viewed from the surrounding environment the colony can be regarded as a superorganism, a large and diffuse ameoboid entity whose ingestive apparatus, comprised of the foraging workers, moves back and forth in circadian pulses over the surrounding territory.’
- qS14.** *Superorganismality*: (*sensu lato*; Wilson & Sober, 1989, pp. 339 and 342) ‘[A]n organism can be defined as “a form of life composed of mutually dependent parts that maintain various vital processes” (Random House dictionary, unabridged edition). . . . We define a superorganism as a collection of single creatures that together possess the functional organization implicit in the formal definition of organism. . . . No differences exist in the fitness of individuals within groups.’
- qS15.** *Superorganismality*: (*sensu stricto*; Seeley, 1989, p. 548) ‘[I]n many species of social insects the female members of a colony (queens and workers) fight over who will lay eggs. In the most advanced species of social insects, however, there appears to be little if any conflict within colonies, so that these colonies do represent superorganisms.’
- qS16.** *Superorganismality*: (*sensu stricto*; Wilson & Sober, 1989, pp. 339, 343); ‘We define a superorganism as a collection of single creatures that together possess the functional organization implicit in the formal definition of organism. . . . When between-unit selection overwhelms within-unit selection, the unit itself becomes an organism in the formal sense of the word.’
- qS17.** *Superorganismality*: (wasps; Queller & Strassmann, 1991, p. 736; consistent with Wheeler, 1911, 1928b) ‘The large, complex, integrated societies of yellowjackets (as well as ants, honeybees, and termites) are often viewed as superorganisms, with workers functioning like a metazoan soma, maintaining the integrity of the colony and promoting its reproduction through the germ line represented by the queen. The superorganism concept does not serve so well for the simpler societies like those of *Polistes*, where individuals often seek their own reproductive advantage, sometimes through dangerous fighting. If a *Polistes* colony is an organism, it is a very peculiar one, with the various body parts elbowing and kneeling each other aside, each vying to become a gonad.’

Table 2. Continued

- qS18. Superorganismality:** (insects; Ratnieks & Reeve, 1992, p. 56, referring to the criteria advocated in qS16) ‘One difficulty with this definition is the point at which “overwhelming” takes place. For example, is it justifiable to call a honey bee colony a superorganism (Seeley, 1989), despite the evidence for “between-unit” conflict over queen-rearing? The existence of this conflict might be enough to withhold use of the term.’
- qS19. Superorganismality:** (insects; Ratnieks & Reeve, 1992, p. 56) ‘[T]he foraging sub-caste of an insect society is likely to show “superorganismic” properties, even if there is actual conflict in other areas of colony life. Synergism may also occur in other vital tasks, such as nest defense, construction, and maintenance.’
- qS20. Superorganismality:** (insects; Maynard Smith & Szathmáry, 1995, pp. 257–258) ‘The resemblance between the development of an insect colony and of an organism has led to the concept of a “superorganism”. The analogy has some value. To the extent that individual ants, bees or termites have lost the capacity to reproduce, they can propagate their genes only by ensuring the success of the colony, just as somatic cells can propagate theirs only by ensuring the success of the organism. Hence, the colony can be expected to have features adapted to ensure its success, and it is reasonable to apply concepts of optimization to it, rather than to the individual – as was done, for example, by Oster & Wilson (1978) in their book on insect caste systems. But for our purposes the concept of a superorganism is of little use. To understand the origins of animal societies, we must ask how individuals capable of reproduction came to cooperate to the extent that most of them lost the ability to reproduce. To understand their maintenance, we must explain why they are not disrupted by cheating.’
- qS21. Superorganismality:** (insects; Wilson & Hölldobler, 2005, p. 13368, consistent with Wheeler, 1911, 1928b) ‘When in evolution does eusociality become irreversible? We infer that this comes very early in the evolution of that condition, in particular when an anatomically distinct worker caste first appears, hence when a colony can most meaningfully be called a superorganism.’
- qS22. Superorganismality:** (*sensu lato*; Hölldobler & Wilson, 2009, pp. 8–9) ‘In the broadest sense, the term *superorganism* is appropriate for any insect colony that is eusocial, or “truly social,” and that means combining three traits: first, its adult members are divided into reproductive castes and partially or wholly nonreproductive workers; second, the adults of two or more generations coexist in the same nest; and third, nonreproductive or less reproductive workers care for the young.’
- qS23. Superorganismality:** (*sensu stricto*; Hölldobler & Wilson, 2009, p. 9) ‘For those who prefer a stricter definition, the term *superorganism* may be applied only to colonies of an advanced state of eusociality, in which interindividual conflict for reproductive privilege is diminished and the worker caste is selected to maximize colony efficiency in intercolony competition.’
- qS24. Superorganismality:** (*sensu lato* and *sensu stricto*; Hölldobler & Wilson, 2009, pp. 513–514) ‘The level of this gradient at which the colony can be called a superorganism is subjective; it may be at the origin of eusociality (preferred by E.O. Wilson) or at a higher level, beyond the “point of no return”, in which within-colony competition for reproductive status is greatly reduced or absent (preferred by B. Hölldobler).’
- qS25. Superorganismality:** (*sensu stricto*; Seeley, 2010, p. 25) ‘[S]election for close cooperation produced the thoroughly integrated societies of cells that we know today, for example, as hummingbirds and human beings. The same sort of selection for extreme cooperation has also happened with some societies of animals to produce the thoroughly harmonious, smoothly running insect societies that we can call superorganisms. These include not just colonies of honeybees but also the gigantic colonies of leafcutter ants, driver ants, or fungus-growing termites.’
- Superorganismality: untenable non-social-insect extensions**
- qN1. Superorganismality:** (general; Park, 1941, p. 164) ‘[A] community may be said to have a physiology – the study of many functions within and of the whole, culminating in a study of what is called the superorganism, recently examined by Emerson (1939).’
- qN2. Superorganismality:** (general; Hartshorne, 1942, p. 254) ‘Now our question is whether a human group is essentially a democracy, a colony of organisms (or a pseudo-super-organism), lacking radical unity and therefore a dominant monad, lacking, that is, a full-fledged group mind that disposes of the members for its own purposes, or whether it is so unified that it can as a whole possess a single individual mind, metaphysically speaking the aristocrat or super-member of the group.’
- qN3. Superorganismality:** (general; Wilson, 1990, p. 138) ‘Envisioning group selection as a process analogous to individual selection therefore makes it quite reasonable that, in certain ecological situations, random associations of individuals can be molded into functionally organized groups – superorganisms in the same sense that individuals are organisms.’
- qN4. Superorganismality:** (global; Lovelock, 2000, Preface) ‘The biosphere is the three-dimensional geographic region where living organisms exist. Gaia is the superorganism composed of all life tightly coupled with the air, the oceans, and the surface rocks.’
- qN5. Superorganismality:** (general; Camill, 2004, p. 1) ‘Forbes saw the community of interacting species in the lake as a complex machine, a superorganism, where order is a natural consequence of proper functioning among its parts. Popularity for the superorganism concept arose, in part, from the search for a unifying conceptual framework for ecology, especially how the interactions among parts of ecological systems (organisms) might lead to emergent properties at higher levels (populations and communities).’
- qN6. Superorganismality:** (humans; Li *et al.*, 2008, p. 2117) ‘Human beings can be considered as “superorganisms” as a result of their close symbiotic associations with the gut microbiota. Superorganism metabolism involves integration of truly indigenous metabolic processes (coded in the host genome) with those of the microbiome.’
- qN7. Superorganismality:** (humans; Duarte *et al.*, 2012, p. 636) ‘Extending understanding from other social neurobiological systems, we argue that considering sports teams as functional integrated “superorganisms” might allow us to capture the self-organized dynamics of complex social interactions that shape collective behaviours in teams.’

Wheeler's (1911) key paper – his first and only in-depth treatment of the superorganism – was not regularly cited during the decades that followed. This does not imply that the article was unread, or that its thesis was rejected, but the citation data suggest that the superorganism hypothesis was accepted passively, or even treated as a truism. As previous authors (e.g. Hölldobler & Wilson, 2009) have pointed out, much of the social insect research conducted in the 1950s and 1960s focused on the chemical (ants and termites) and acoustic or tactile (bees) basis of social coordination. This work transformed our understanding of social insect biology, but it is difficult to see how the honeybee dance language (Von Frisch, 1956) or the first identification of substances such as brood and trail pheromones (Wilson, 1959, 1965) could have been seen as a challenge to the idea that colonies are superorganisms (see e.g. Lüscher, 1953), and thus have justified the abandonment of Wheeler-superorganismality in the second half of the 20th century.

Wheeler himself rarely made use of the superorganism in the major works he published after 1911, and other research ignored it almost entirely (e.g. Bailey, 1920; Brian, 1965; Donisthorpe, 1927 – notwithstanding this leading British myrmecologist of the time dedicating his book to Wheeler; Elton, 1932). After an early approving discussion by Huxley (1912) (Table 2, qS5) only Alfred Emerson set out to elaborate directly upon Wheeler's ideas (Emerson, 1939, 1952). Some have claimed the problem was not that the notion of intra-colony integration was controversial (e.g. Lumsden, 1982), but that the superorganism appeared to offer 'no techniques, measurements, or even definitions by which the intricate phenomena in genetics, behavior, and physiology can be unraveled' (Wilson, 1967, p. 31, 1971). However, that seems a strange criticism, as no biologists abandoned Weismann's proposal that metazoans are characterized by germ-line and soma because it offered no reductionist hypotheses about the developmental biology of cell lineages. As noted by Folse & Roughgarden (2010), Weismann (1893) was probably the first to see the clear parallels between organismal and superorganismal germ-line and soma (Table 2, qS1). This precise insight was later lost when, following Wheeler's death, the colony-as-superorganism thesis was transformed by others into a holistic metaphor meant to imply that homeostasis can be found at all levels of biological organization (Wilson, 1967; Cronin, 1991) (e.g. Table 2, qN1 and qN2). As summarized by Wilson & Sober (1989), the demise of the superorganism was celebrated as a major achievement by social insect experts and general evolutionary biologists alike, but the idea researchers set out to overthrow was a grossly distorted caricature of the original Wheeler version.

Subsequent efforts to reinstate the superorganism have clearly been successful, as the superorganism meme is now well established in the literature, but one cannot claim that the concept was 'resurrected' without specifying to what extent new versions resemble Wheeler's (1911) original (Mitchell, 1995). There is in fact very little similarity because the original hypothesis was lost in translation during the last decades of the 20th century and replaced by alternatives that

were either less precise or overly precise, and not generally agreed upon. It is telling that even *The Superorganism*, a monograph that is often credited with completing the revival of the colony-as-superorganism thesis (Hölldobler & Wilson, 2009), presents the concept in three incompatible forms, all of which differ from Wheeler's original version (Table 2, qS22–24) that the authors had tacitly endorsed a few years earlier (Wilson & Hölldobler, 2005) (Table 2, qS21). On a more fundamental level, whereas Wheeler sought to establish a comparative research program in which social insects with physically differentiated castes could be used as models for understanding complementary integration of cells in multicellular organisms (Table 2, qS6; see also qS10 and qS11), contemporary authors have often used the term superorganism to emphasize awe-inspiring but idiosyncratic aspects of social organization (but see Helanterä, 2016).

(2) The general demise of conceptual transparency from the 1980s onwards

As we noted already, Wheeler's emphasis on physical queen–worker caste differentiation was never shown to be misplaced, but was simply abandoned to make room for 'modern' biological practices that focused primarily on proximate mechanisms of behaviour, genetics and ecology. The key evidential sources cited in Wilson (1971, p. 318) to justify the dismissal of the superorganism appear to be critiques of the teleological and anthropomorphic elements that others had added to it (Novikoff, 1945), perhaps partly induced by Wheeler's later (1928) writing which was less conceptually stringent than his early (1910, 1911) work (Cronin, 1991). The unfortunate consequence was that the ultimate questions about the emergence of nature's obvious layers of hierarchical complexity that had inspired many of the pioneering evolutionary biologists also disappeared from the centre stage. They would not re-emerge until the mid-1990s and by then the scientific landscape had substantially changed. In 1975, the sociobiology approach had billed itself as 'the systematic study of the biological basis of all social behaviour' (Wilson, 1975, p. 4), often emphasizing loosely defined functional similarities that would easily allow inferences about humans and other social animals to be drawn (Table 1). In the same year, inclusive fitness theory (Hamilton, 1963, 1964a,b) obtained its fully general form based on the Price equation (Hamilton, 1975; Dawkins, 1976; Harman, 2010), but it took years for this levels-of-selection framework for understanding social evolution to become integrated with the sociobiology approach (Keller, 1999), which continued to embrace ambiguous definitions of eusociality and superorganismality (e.g. Table 2, qS13). When calls for the return of the superorganism first emerged in the 1980s (Lumsden, 1982; Seeley, 1989; Wilson & Sober, 1989), and 1990s (Seeley, 1995), and then subsequently gained momentum in the early 2000s (Hölldobler & Wilson, 2009), they were rooted in the convenience definitions of sociobiology that were explicitly at odds with the original concepts of eusociality (Batra, 1995) and superorganismality (Wheeler, 1911).

On the very first page of the article in which she defined eusociality, Batra (1966a) clearly noted that there is a fundamental difference between halictid bee eusociality with plastic helper roles, and the social systems of honeybees and stingless bees, where all colony members belong to one of two distinct, physically differentiated castes (Table 2, qE8). Or, as Crespi & Yanega (1995, p. 109) suggested, 'The primary reason that the definition of eusociality takes its present form is that it was developed for halictine bees in particular and borrowed for social arthropods in general'. Had Batra's (1966a) paper not been devoted exclusively to halictid bees, one would almost have expected her to have identified the stingless bees and honeybees as a separate superorganismic domain (Table 2, qE14 and qE19), perhaps even quoting Wheeler (1911).

With the superorganism having been dismissed as a misnomer of unscientific holism (Wilson, 1967), it is perhaps no surprise that Michener (1969, 1974) coined the term 'highly eusocial' for species with physically differentiated castes, rather than employing the term 'superorganism' (Table 2, qE10 and qE11). His classification is functionally reminiscent of Wheeler-superorganismality, which some other scholars continued to use correctly until the middle of the 20th century (Table 2, qS10 and qS11) (later Emerson papers become much more opaque; Cronin, 1991). However, whereas Weismann, Huxley, Wheeler and Batra had inferred that advanced colony life could evolve only subsocially by offspring staying to help a single (pair of) founding parent(s) (Table 2, qE1, qE3, qE4 and qE8), Michener argued that high-level eusociality could also evolve para(semi)socially (Table 2, qE9), i.e. by aggregation of same-generation colony founders (Lin & Michener, 1972; West Eberhard, 1975). An earlier version of that extension had triggered explicit scepticism by Hamilton (1964b) and Michener (1985) subsequently re-invoked this argument, but in rather technical terms which largely prevented the message from reaching researchers lacking specialized knowledge of the biology of bees. A further historical misfortune is that Michener (1969, 1974) cited the wrong article (Batra, 1966b), which effectively left the original eusociality concept (Batra, 1966a) orphaned for non-bee biologists. Moreover, almost no one noticed Batra's own attempts to set the record straight when she later coined the term 'hypersocial' for honeybees and stingless bees to acknowledge the significance of their physically differentiated and completely mutually co-dependent castes (Batra, 1977, 1995) (Table 2, qE14 and qE19).

In this light, it is not surprising that eusociality and superorganismality could only be haphazardly connected to the major transitions in evolution paradigm that emerged in the 1990s. Evolutionary biologists with a passing interest in social insects could do little else than consider eusocial animals *sensu* Wilson (1971, 1975, 1985) as a single, homogenous group. Writing in an era when synthesis monographs by specialists gave them no reason to believe otherwise (Table 2, qE12, qE13, qE15 and qS13), Maynard Smith & Szathmáry (1995) drew the conclusion that the origins of eusociality *sensu* Oster & Wilson (1978) constitute major evolutionary transitions (Table 2, qE18, qS13, qS20).

By defining the first emergence of insect colonies as major transitions independent of individual commitment, their book did a great deal to popularize the claim that essentially all Wilson-eusocial insects have transitioned beyond the level of metazoan multicellularity simply because they form 'societies'. However, by not being specific on the criterion of physically distinct queen-worker polymorphism, readers were left with confusion about the colony-as-superorganism thesis. In retrospect, this may have been a choice between a rock and a hard place, i.e. between a sociobiological superorganism concept that had become distorted to the point of being meaningless and an alternative formulation based on untenable group-selection logic (Wilson & Sober, 1989) that Maynard Smith would have found principally unacceptable (Maynard Smith, 1987) (Table 2, qS14). By their endorsement of catch-all Wilson-eusociality as a broad putative transition towards some form of higher complexity (Table 2, qE15 and qS20), Maynard Smith & Szathmáry (1995) inadvertently opened a Pandora's box filled with difficulties associated with unspecified emergent properties and appeals to reproductive harmony (Wilson & Sober, 1989) (Table 2, qS14). At the same time, they also sidestepped the more coherent but overly restrictive conflict-regulation version of superorganismality by Seeley (1989) that had gained considerable traction by 1995 (Table 2, qS15) (see Sections II.3–5 for further details).

(3) 'Resurrected' superorganism hypotheses never received a solid conceptual foundation

Once the sociobiology definition of eusociality (Wilson, 1971, 1975, 1985) took hold, the notion that morphologically distinct castes represent a special state of organizational complexity faded from professional consciousness. Caste differentiation became based on purported behavioural differences (Table 2, qE12, qE13 and qE15), lumping together foraging by morphologically differentiated castes, reproductive skew contests in dominance hierarchies, and age-specific behavioural differences (Peeters & Crozier, 1988). This made 'caste' applicable to almost any social organism, and relaxed the need to consider that morphological caste differentiation requires complete and evolutionarily irreversible genetic rewiring of exceedingly complex developmental pathways to create an integrated higher level 'social physiology' (Wheeler, 1986; Johnson & Linksvayer, 2010). Physically differentiated queen and worker castes are thus incomparable with other forms of Wilsonian 'caste' that are merely expressions of phenotypic plasticity (West-Eberhard, 1989) which can reverse over both developmental and ecological time. Although plasticity can create substantial differences between phenotypes with the same genotype, there is a point where morphological caste differences need to acquire distinct hardwired developmental pathways to diverge further into forms that are fixed for adult life (Wilson & Hölldobler, 2005; McShea, 2015). The comparative data unambiguously support that behavioural 'castes' always precede true morphological castes over evolutionary time, and that there have been no reversals (but merely

occasional lateral reductions; Table 2, qE7) to the ancestral monomorphic and phenotypically plastic states after the evolution of physical germ–soma caste differentiation (Boomsma, 2013).

From the 1980s onward, broad-brush eusociality came to be regarded as the most advanced type of social organization found across *all* animal lineages – a remarkable and even greater deviation from Batra's original definition (Table 1). Smooth-continuum thinking was driven to extremes in the mid-1990s (e.g. Gadagkar, 1994; Keller & Perrin, 1995; Sherman *et al.*, 1995) (e.g. Table 2, qE16), in spite of pleas to exercise restraint when applying the term 'eusociality' (Peeters & Crozier, 1988; Kukuk, 1994; Crespi & Yanega, 1995; Beekman, Peeters & O'Riain, 2006) (e.g. Table 2, qE20). This is all the more puzzling because, upon closer inspection, two of the three catch-all criteria for the sociobiology version of eusociality (Wilson, 1971) are ambiguous in species with physically differentiated queen and worker castes: (i) generation overlap – helpers can no longer be considered true generations when they are obligatory sterile in the presence of their mother queen, which is universally true in the higher termites (Higashi *et al.*, 1991) and often a correct approximation in the ants and corbiculate bees (Hammond & Keller, 2004; Ratnieks & Helanterä, 2009), and (ii) cooperative brood care – it becomes a stretch to continue calling brood care cooperative in the traditional sense when reproductives are isolated in royal cells (higher termites) and domesticated for egg production by life-time unmated workers. The latter is not only typical for higher termites, ants and perennial corbiculate bees, but also for short-lived colonies of bumblebees and vespine (yellowjacket) wasps, where workers manage their domesticated queen towards the end of the colony life cycle by killing or abandoning her at the best possible moment for maximizing their own inclusive fitness (Bourke, 1994; Loope, 2015). Apparently, when the third criterion for sociobiological eusociality – reproductive division of labour – has become manifest as irreversible morphologically distinct caste fate for all colony members, the two other criteria lose the meaning they had for cooperative breeders. This is what one would expect when physical germ–soma caste differentiation marks an irreversible major evolutionary transition, and thus aptly illustrates that glossing this over made it very difficult to see the major transition woods for the broad-brush eusocial superorganism trees.

Coincident with the emergence of new superorganism concepts in the 1980s, researchers inspired by the seminal work of Trivers & Hare (1976) began using Hamiltonian inclusive fitness principles to test systematically for the expression of reproductive conflicts in social insects (e.g. Herbers, 1984; Bourke, 1988; Ratnieks, 1988; Boomsma & Grafen, 1990; Bourke & Franks, 1995; Crozier & Pamilo, 1996). Over time, a large body of empirical research accumulated, demonstrating that reproductive conflicts between hymenopteran workers and queens over sex allocation and male production are ubiquitous. These conflicts often result in one caste enhancing its inclusive fitness at the expense of the other (Ratnieks,

Foster & Wenseleers, 2006; Meunier, West & Chapuisat, 2008). Less general, but equally significant conflicts over caste fate were added later (Bourke & Ratnieks, 1999), and more recently conflicts between stored ejaculates and their ensuing patriline (Sundstrom & Boomsma, 2001; Hughes & Boomsma, 2008; Galbraith *et al.*, 2016) also came to light. Reproductive allocation conflicts of this kind are found in both superorganismal and non-superorganismal lineages *sensu* Wheeler. For example, relatedness-asymmetry-induced split sex ratios have been documented in halictid bees by Mueller (1991), in epiponine wasps by Strassmann, Sullender & Queller (2002) and in *Formica* ants by Sundström (1994) and Sundstrom, Chapuisat & Keller (1996), confirming that social insect helpers/workers can successfully attempt to enhance their own inclusive fitness, and thereby reduce the fitness of egg layers, at all levels of hierarchical organization. To give a further example of conflict in seemingly harmonious superorganisms, if honeybee workers emerge during the short window of queen replacement, their prospective indirect fitness from nursing a new queen's offspring will be only half of what it would otherwise have been. In response, such workers express selfish traits that are not in the interest of the colony, and they 'plan' these phenotypic switches in the pupal stage (Woyciechowski & Kuszewska, 2012), similar to what may happen to regulate queen number in epiponine wasps (Strassmann *et al.*, 2002). Reproductive allocation conflicts are thus omnipresent, both in superorganismal and non-superorganismal hymenopteran colonies. These repeated confirmations of kin conflicts predicted by inclusive fitness theory were important advances for understanding social cooperation from first principles (Bourke & Franks, 1995; Crozier & Pamilo, 1996), but they also helped to establish the notion that reduction or regulation of such conflicts had to be a necessary condition for becoming superorganismal, a contention that we will argue is incorrect in Section III 3.

Once Wheeler-superorganismality had been dismissed and sociobiological eusociality taken for granted, researchers could only look for superorganisms at the beginning or towards the end of the Wilson eusociality continuum. These approaches gave birth to a new *sensu lato* superorganism (all social insect colonies are superorganismal) for those primarily inspired by Oster & Wilson (1978), Wilson (1985) and Maynard Smith & Szathmáry (1995), and a new *sensu stricto* superorganism (only some of the advanced lineages which have both physical caste differentiation and evolutionarily derived conflict management are superorganismal) for those working on colony physiologies of honeybees or ants (e.g. Seeley, 1989; Moritz & Southwick, 1992; Bonabeau *et al.*, 1997) (Table 2, qS24). We have summarized our interpretation of these historical events in Fig. 1, illustrating the distinct social categories proposed by Wheeler (1911), Batra (1966a, 1977), and Michener (1969) to the left, the Wilsonian eusociality continuum concept in the middle, and the three competing superorganism concepts of the last ca. 40 years to the right. It is clear that only Wheeler's superorganism concept constitutes a fully operational scientific definition,

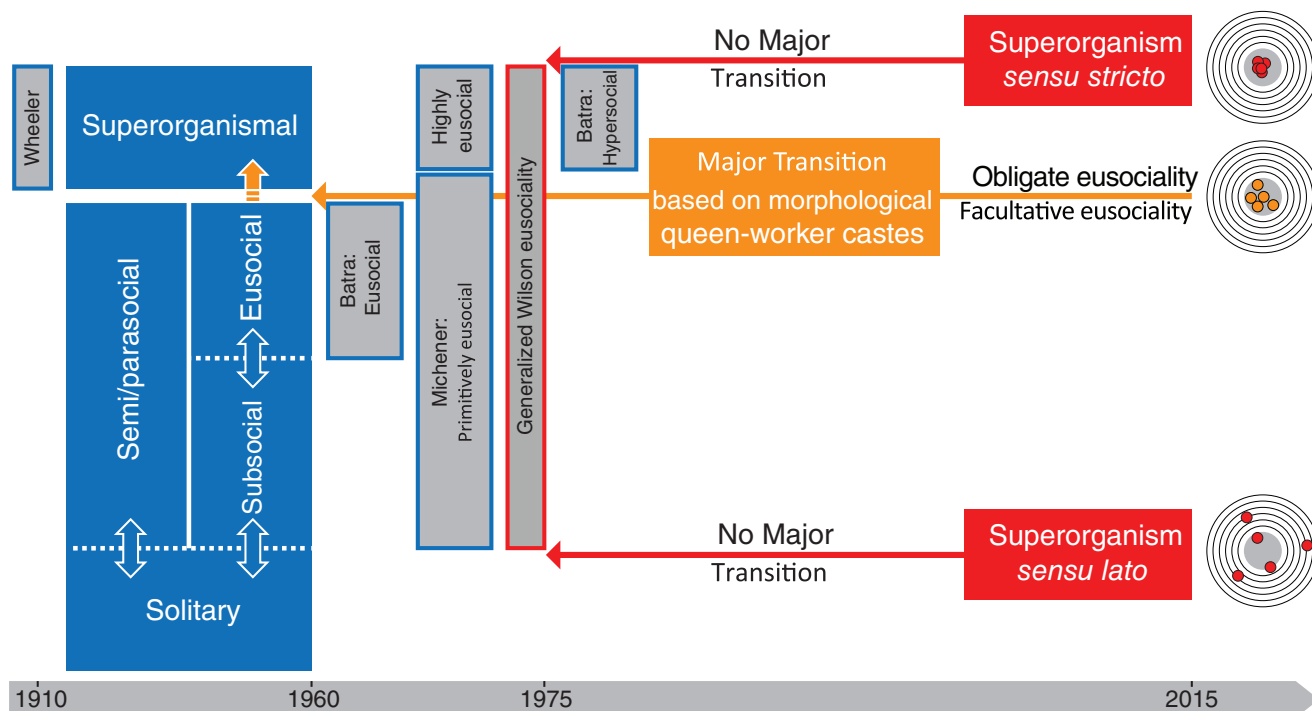


Fig. 1. A century (bottom time line) of sociality and superorganismality concepts with commonly used social categories in blue boxes and their coverage by definitions as grey boxes with coloured frames. Wheeler (1911) pursued a top-down categorization stipulating that physically differentiated queen and worker castes characterize a superorganismal level of hierarchical complexity beyond solitary insect organismality (orange arrows and box). Batra (1966a, 1977) and Michener (1969) defined stages of social evolution bottom-up by contrasting subsocial, semi/parasocial and eusocial colonies without morphologically distinct castes and the highly (hyper)social lineages represented by the perennial honeybees and stingless bees, but not by the annual bumblebees which remained (albeit ambiguously) as primitively eusocial bees in spite of their physically distinct queen and worker castes. After initially keeping all transitional stages between the blue boxes open, Michener (1985) eventually reached the same conclusion as Wheeler (1911) that the ancestors of highly eusocial/superorganismal lineages were sub/eusocial (offspring staying with their mother) rather than semi/parasocial (multiple same-generation females engaging in cooperative breeding). Vertical double-headed blue arrows indicate phylogenetically reversible transitions and the orange single-headed arrow illustrates irreversible major evolutionary transitions to superorganismality based on all colony members having a single, morphologically differentiated caste phenotype for life. Wilson's (1971, 1975) merging of all non-solitary animals into a single eusociality gradient (grey box with red frame) caused the major transitions based on morphologically differentiated queens and workers to become conceptually hidden (i.e. the grey box with the red frame interrupts the horizontal orange arrow in a much more fundamental way than Batra's and Michener's ambiguity about bumblebees). This induced a quest for the rediscovery of superorganismality either at the start of the sociobiological eusociality range or towards the end (red horizontal arrows and boxes), yielding two kinds of new superorganism concepts, a *sensu lato* one assuming that all loosely defined eusocial systems (Wilson, 1971, 1975) are superorganismal, and a *sensu stricto* one assuming that only large and supposedly harmonious colonies are proper superorganisms (Seeley, 1989; Wilson & Sober, 1989). However, only the Wheeler version of the superorganism (orange text box) appears to be precise relative to a grey target (circle towards the right) that can be reconciled with an irreversible major transition because the emergence of 100% commitment to a single physical caste phenotype for life is known (e.g. Wilson & Hölldobler, 2005) and expected (Boomsma, 2013) to be a point of no return. The new *sensu lato* superorganism concept is very imprecise because it targets essentially all social systems (cf. Batra, 1995; Table 2, qE19) without discriminating between them (e.g. Wilson, 2012, 2014), suggesting that all of these are products of comparable major evolutionary transitions (Table 2, qS24). The new *sensu stricto* superorganism concept developed by Seeley (1989) is merely overly precise relative to the grey target in focusing only on derived superorganismal elaborations while excluding ancestral superorganisms, such as bumblebees and vespine wasps with life-time physically differentiated caste fates, that are closer to the putative ancestral lineages with small full-sibling colonies that originally made the transitions.

because it unambiguously stipulates that all and only social systems with morphologically differentiated castes qualify. The straightforward classification by Wheeler corresponds to what Crespi & Yanega (1995) and Boomsma (2007, 2009, 2013) coined 'obligate eusociality' to make explicit that all individuals in a colony commit for life to a single adult caste

phenotype. These lineages are fundamentally different from their facultatively eusocial counterparts, where a number of colony members always retain reproductive totipotency (Crespi & Yanega, 1995), which is incompatible with being Wheeler-superorganism (Fig. 1; Table 2, qE17, qE21 and qE22).

(4) The new *sensu lato* superorganism hides the transitional points of no return

Many arguments can be lined up to document that the *sensu lato* superorganism hypothesis (Oster & Wilson, 1978) fails to identify irreversible (point of no return) transitions in hierarchical complexity. This rendition of the superorganism appears to be mostly based on shallow analogies, e.g. on notions such as castes being like organs, or nests being a colony's analogue of a skeleton (Monceau, Bonnard & Thiery, 2013) or skin (Hölldobler & Wilson, 2009), which cannot be used without specifying that these criteria would fail in colonies where caste remains plastic or nests ephemeral. As outlined by Ratnieks & Reeve (1992), there is no unambiguous answer to the question of how many organism-like traits a colony must possess to be a superorganism (Table 2, qS18) and there are many lineages that qualify as eusocial *sensu* Wilson for which there is no analogy at all with Wheeler superorganismal colonies (see e.g. Queller & Strassmann, 1991) (Table 2, qS17). It is in fact surprising that social adaptations became characterized in such a loose narrative manner less than 10 years after Williams (1966) had lined up very stringent parsimony arguments for the functional interpretation of putative higher-level adaptations (Boomsma, 2016). Two decades earlier, Schneirla (1946, p. 391) had also correctly noted that instead of 'relying upon a method of analogy in studying social levels, stressing apparent but unclear similarities, it is preferable to compare phenomena by looking for the basis of both similarities and differences and endeavoring to emphasize these according to their respective importances'.

It is crucial to note that polistine wasps and naked mole rats have caste phenotypes that are principally temporal, while reproductive privileges are doled out by physical necessity in ants, honeybees, and vespine wasps, as well as other lineages where all colony members have a distinct caste phenotype for life. Morphologically distinct queen and worker castes have higher-level germ-line and soma functions, while polistine dominance hierarchies remain similar to cooperatively breeding vertebrates (Crespi & Yanega, 1995; Boomsma, 2007, 2013), where high-ranking egg layers induce ovary regression in lower ranking females, but without causing the permanent loss of reproductive totipotency (e.g. Jeanne, 1980). Dormant ovary function thus remains reversible, and removal of the dominant breeder reshuffles the hierarchy of inseminated breeders (Strassmann *et al.*, 2002). Not so in systems where workers are life-time unmated and queen pheromones are honest signals of fertility (Keller & Nonacs, 1993; Holman *et al.*, 2010). Distinctions of this kind are also decisive for understanding sequestered multicellular germ lines, which are uniquely unitary in all but the most basal metazoans (Barfield, Aglyamova & Matz, 2016), but recurrent in modular vascular plants, macroscopic algae, and multicellular fungi (Buss, 1987; Clarke, 2011; Lang & Rensing, 2015). Not making a similar distinction within the sociobiologically defined eusocial insects is equivalent to thinking that post-menopausal human females can regain fertility by turning ovarian fat cells into eggs. Unique colony

germ lines, as provided by the inseminated founding queens of ants, bumblebees and vespine wasps, and the founding pairs of termites, are protected against external danger by colony workers as soon as these emerge, a service that became continuous in the evolutionarily derived swarming honeybees, stingless bees and *Provespa* wasps (Boomsma, Huszár & Pedersen, 2014). Such somatic worker functions are not found in *Polistes* colonies, where workers often challenge reproductive dominants, forcing them to defend their monopoly (Table 2, qS17) – if their egg layers were to be germ lines they would be analogous to human eggs risking death to aid in immune defence against sexually transmitted disease. This argument extends into the swarm-founding epiponine wasps where the share of swarming inseminated breeders in a colony's later reproductive success is unpredictable (Strassmann *et al.*, 2002).

In sum, the animal lineages that display the three defining characteristics of Wilson-eusociality (cooperative brood care, reproductive division of labour, generation overlap) are so heterogeneous in their degrees of cooperative breeding and reproductive altruism that common-cause superorganismal traits indicative of major evolutionary transitions cannot be identified across lineages. As long as all, most, or some individuals have retained the totipotent capacity to mate and raise offspring of both sexes, they will do so whenever an opportunity arises. This is fundamentally different from superorganismal systems *sensu* Wheeler, where nursing colony members never mate and breeders always mate but never re-mate later in life (Boomsma, 2007, 2009, 2013). The *sensu lato* superorganism concept (Wilson, 1971, 1975, 1985; Oster & Wilson, 1978) must therefore be incorrect. At best some of the lineages identified by this concept have evolved a level of organization distinctly beyond metazoan multicellularity.

(5) The new *sensu stricto* superorganism misplaces the transitional points of no return

The *sensu stricto* hypothesis was proposed by Wilson & Sober (1989) and Seeley (1989), but in very different ways. Wilson & Sober (1989) thought that group selection always had the potential to produce perfectly harmonious group adaptations (see also Wilson, 1990; Table 2, qS14, qS16, qN3), a contention that is incompatible with a recent model specifically designed to capture the superorganism from first principles (Gardner & Grafen, 2009), and a wealth of accumulated empirical evidence (see Bourke, 2011a, b for recent reviews). Seeley (1989) acknowledged reproductive conflicts, but assumed that harmonious superorganisms like the honeybee arose by regulating these conflicts (Table 2, qS15, qS25). The problem with both of these approaches is that reproductive harmony is not a discrete colony-level trait that is either present or absent, but a complex set of variables determined by interactions between queens and nursing workers who consistently act in their own best inclusive fitness interest (Ratnieks & Reeve, 1992) (Table 2, qS18 and qS19). Closer scrutiny also reveals that the notion of 'cooperative harmony' is incompatible with honeybee drones often

being ‘slaughtered by their industrious and sterile sisters’, a behaviour that was documented over 150 years ago (Darwin, 1859, pp. 202–203; see also Kirby & Spence, 1818). As Cronin (1991, p. 308) emphasized more recently, honeybee social life can be described rather unsympathetically as mother queens killing offspring queens, older sister queens killing hatching younger siblings, and workers killing their brothers. It is this alternative picture which appears to be supported both by inclusive fitness theory and empirical studies (Ratnieks & Reeve, 1992; Ratnieks & Helanterä, 2009). This does not imply that lineages like honeybees with advanced colony-level adaptations such as collective thermoregulation or dance language are not superorganismal (Ratnieks & Reeve, 1992) (Table 2, qS25). The issue is that neither the presence of potential conflict at the origin of a major transition, nor the magnitude of expression of actual conflict in later superorganismal elaborations can be used to decide whether a lineage is superorganismal or not (Table 2, qS18 and qS19) (see Section III.3).

The only viable criterion for understanding superorganismal origins as evolutionarily irreversible transitions is Wheeler’s dichotomous character of morphologically differentiated caste fates for all colony members (Fig. 1). Less spectacular basal branches or sister lineages of evolutionarily derived superorganisms such as honeybees, army ants, leaf-cutting ants and *Macrotermes* fungus-growing termites must therefore also have transitioned beyond metazoan organismality when their morphological caste traits unambiguously indicate life-time unmatedness for all workers. *Sensu stricto* superorganismality thus remains blind for superorganismal origins (Bourke, 2011a; Clarke, 2014), and fails to acknowledge that potential reproductive conflict (Ratnieks & Reeve, 1992) is fundamentally innate to superorganisms (Table 2, qS18 and qS19), just like nuclear–cytoplasmic conflict is to multicellular plants and animals. Buss (1987) gives examples of conflicts between germ line and soma in basal metazoan branches where somatic cells retain the capacity to produce gametes. However, closed germ lines and complex organismality appear to be universally present in the Bilateria, and likely arose already in the Cnidaria (Barfield *et al.*, 2016), suggesting by analogy that hymenopteran superorganismal origins required effective queen-policing of worker egg laying. Until the terminal phase of colony decline, this seems a reasonable inference because colonies must have been small and annual at the origins of superorganismality (e.g. Ratnieks & Reeve, 1992; Zanette *et al.*, 2012).

For the same reason, superorganismal elaborations with substantial non-suppressed conflict cannot be taken as evidence for superorganismality being compromised. What matters is that these conflicts did not affect the loss of matedness totipotency in both queens and workers – the hallmark trait of an irreversible transition to superorganismality. Thus, queen- or male-culling traits do not make stingless bees, honeybees, or Argentine ants non-superorganismal (Keller, Passera & Suzzoni, 1989; Cronin, 1991; Wenseleers & Ratnieks, 2004; Wenseleers *et al.*, 2005), just like occasional plant species that suffer

from cytoplasmic male sterility do not lose their obligatory multicellular status (Couvet, Ronce & Gliddon, 1998). In the same vein, conflicts due to meiotic drive or genomic imprinting (Burt & Trivers, 2006; Galbraith *et al.*, 2016) have no bearing on the extent to which a lineage is organismal or superorganismal.

Unlike the untenable *sensu lato* version of the superorganism, the *sensu stricto* superorganism is merely incomplete in its coverage. The targets towards the right in Fig. 1 summarize the precision arguments for this contention. They illustrate that the *sensu lato* superorganism targets too many social systems and the *sensu stricto* superorganism too few because it excludes superorganisms that have remained closer to the transitional origin of a lineage-specific point of no return, such as the bumblebees and vespine wasps.

(6) Back to the origins of superorganismality, (un)matedness and Hamilton’s rule

Using the terminology of Crespi & Yanega (1995) (Table 2, qE17), Boomsma (2007, 2009) (Table 2, qE21 and qE22) postulated that strict ancestral monogamy is a necessary general condition for making transitions from facultative eusociality to obligate eusociality *sensu* Crespi & Yanega (1995), and that only some social insects – the ants, crown-group corbiculate bees, vespine wasps, and higher termites – have independently and irreversibly entered the hard-wired caste domain beyond metazoan multicellularity (Fig. 1; Table 2, qE15 and qE16 *versus* qE17, qE21 and qE22). Comparative analyses have confirmed life-time ancestral monogamy in the social Hymenoptera (Hughes *et al.*, 2008), and the same pivotal turning point was shown to apply to the transition between lower and higher termites (reviewed in Boomsma, 2013). However, these reviews left the connection with superorganismality open-ended, and Boomsma (2013, p. 2) erroneously credited Batra (1966a) for defining eusociality as being based on morphological caste differentiation. After our present historical analysis of eusociality and superorganismality, the conclusion must be that hypersociality *sensu* Batra (1977) and obligate eusociality *sensu* Crespi & Yanega (1995) and Boomsma (2007, 2009, 2013) are functionally identical to superorganismality *sensu* Wheeler (1911), defined by permanent membership of each colony member to a single morphologically distinct adult caste that is fixed for life during early individual development (Wheeler, 1986; Helanterä, 2016) (Fig. 1; Table 2, qE17, qE21, qE22, qS3, qS6 and qS7).

The key methodological mantra of the sociobiology approach is that we should use ‘the same parameters and quantitative theory ... to analyse both termite colonies and troops of rhesus macaques’ (Wilson, 1975, p. 4), but such an approach becomes misleading when crucial caste-type distinctions that were broadly acknowledged throughout the history of evolutionary biology (Weismann, 1893; Wheeler, 1911, 1923; Huxley, 1912, 1930; Fisher, 1930; Williams, 1966) are glossed over. One of the more unfortunate consequences of the broad-brush eusociality concept is the fact that it removed the essential Batra-meaning of the term

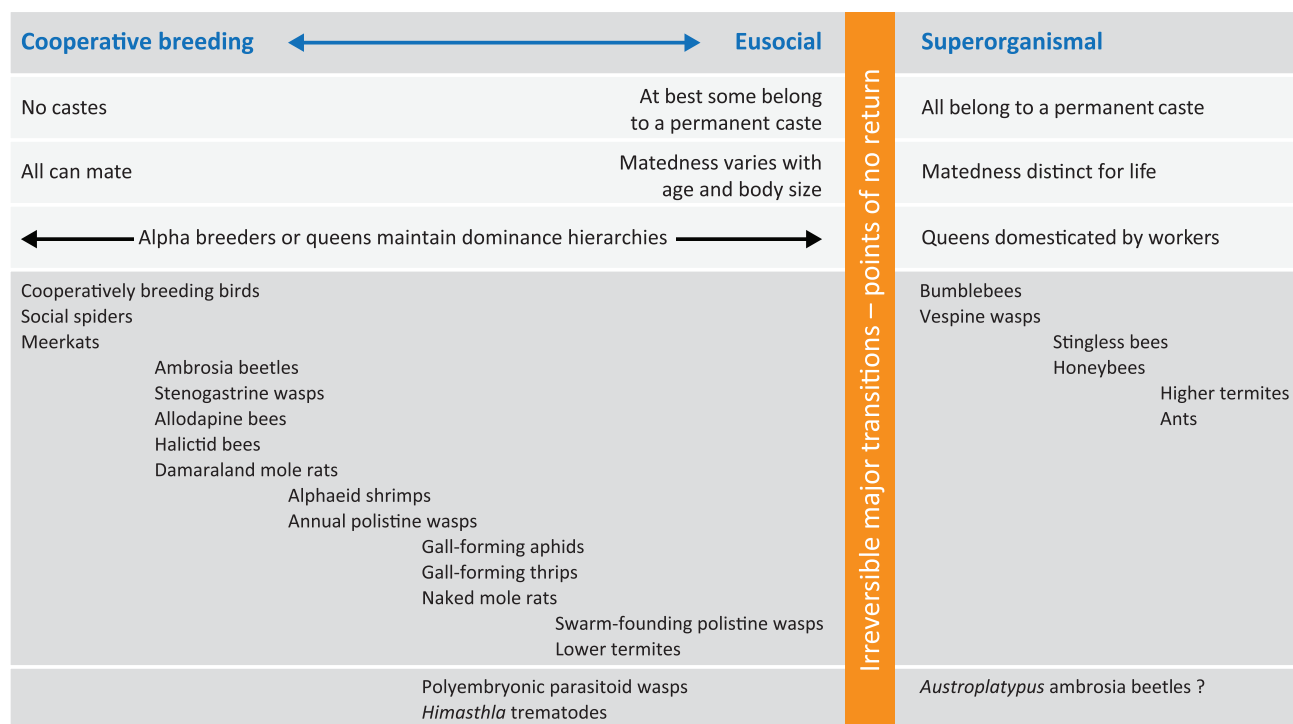


Fig. 2. The superorganismal social insects and a representative selection of non-superorganismal social insects and (in)vertebrate cooperative breeders, separated by the evolutionarily convergent point of no return barrier (orange bar) representing the morphologically differentiated queen–worker caste transitions in the social Hymenoptera and the termites. The three key criteria of caste phenotype, caste (un)matedness, and breeder dominance/domestication are given in the upper section of the diagram and animal lineages are ranked from left to right in the middle section using approximate weighted averages of reproductive skew and social coherence/longevity of colonies across the cooperative breeding–eusociality range (left of the orange bar) and of the degree of distinct morphological caste differentiation and superorganismal ‘germ-line’ longevity (right of the orange bar). Superorganismal entries are broadly representative of most recent ancestral states, and do not take into account that secondary reductions may sometimes have lost or modified castes, because none of these ever represent reversals to an ancestral state of matedness totipotency, which is universally present in either some or many colony members at the other side of the orange bar (Boomsma, 2013). At the bottom left we have listed polyembryonic wasps (Giron *et al.*, 2004) and trematodes (Hechinger, Wood & Kuris, 2011) with altruistic soldier castes that have been called ‘eusocial’, but are not fully comparable with the animals in the middle section because they live within compartmentalized hosts rather than in their own nests or burrows; their parasitism has also induced complexity reductions analogous to those in parasitic myxozoan Cnidaria which are reduced multicellular eukaryotes (Chang *et al.*, 2015), not reversals to protist unicellular life (*cf.* Table 2, qE7). At the bottom right, we have listed the ambrosia beetle *Austroplatypus incomptus*, whose status as an incipient superorganism remains to be confirmed. We did not include marine hydrozoans such as *Physalia* (Portuguese man o’ war) and *Nonomia* cnidarians (Bourke, 2011a) because they have modular growth, and thus no early sequestered single germ line, and they lack the mesoderm that would normally produce most animal organs (Collins *et al.*, 2006).

(*cf.* Batra, 1995; Table 2, qE14 and qE19), and subsequently synonymized eusociality with a *sensu lato* superorganismality concept that is grossly imprecise (Fig. 1). Confusion of this kind goes a long way in explaining why Maynard Smith and Szathmáry (1995) (Table 2, qS20) were so dismissive of the concept of superorganismality. The generalized Wilsonian concepts of eusociality and superorganismality that were prominent in the literature towards the turn of the century prevented them from seeing the obvious point of no return major transitions marked in orange in Fig. 1. They unsuccessfully tried to resolve the issue by suggesting that organisms are able to follow the red (*sensu lato*) pathway to superorganismality displayed at the bottom of Fig. 1, even though the emergence of facultative reproductive altruism in

chimeric groups (Table 2, qS20) has no obvious connection with their major transitions framework. Issues of this type demonstrate that terminological adjustments based on the original meaning of eusociality and superorganismality are not merely a matter of semantics. Rather, the systematic classification of the stages of social evolution developed by early naturalists (Table S2, qS1, qS8, qS10 and qS11) facilitates straightforward understanding of the generality of the ‘gene’s eye’ Hamiltonian perspective that nature has never produced any form of lasting cooperation that does not have inbuilt potential for conflict (Hamilton, 1996). It is only after the catch-all sociobiology concept of eusociality became entrenched that researchers lost sight of the fact that lineages with phenotypically plastic behavioural castes and those

with morphologically differentiated castes represent mutually exclusive hierarchical domains of social evolution (Fig. 1), separated by irreversible major transitions. In other words, once a lineage has become Wheeler-superorganismal it is no longer Batra-eusocial, although it has that ancestry (Fig. 1). Figure 2 illustrates how the social evolution landscape can be mapped to do justice to having either full morphological caste differentiation, some morphological caste differentiation (e.g. specialized soldiers before true workers evolve, as in the lower termites), or no morphological caste differentiation.

Universal life-time unmatedness of helper castes unites the haplodiploid superorganismal ants, corbiculate bees and vespine wasps with the diploid superorganismal higher termites, underlining that the exclusive presence of unmated workers as altruistic helpers of specialized parental reproductives is the key higher-level adaptation that defines the origins of all fraternal transitions to superorganismality (Fig. 2). The logic is that life-time monogamous commitment between parents breeds life-time commitment to unmated soma roles in offspring, because outbred monogamy secures exact equality in gene-copy currency of reproductive success *via* offspring (r_o) and average siblings (r_s) (Boomsma, 2007, 2009). This 'bioeconomic' insight was implicitly acknowledged both by Williams & Williams (1957) and Hamilton (1964b) (see also Marshall, 2015), but needs to be made explicit by recognizing that immediately preceding and often continuing after irreversible transitions, Hamilton's rule ($br_s > cr_o$) reduces to $b/c > 1$. Note, however, that achieving a major transition is not assured with strict relatedness equivalence, as the initially small benefit of raising siblings (b) relative to the costs of foregoing offspring (c) needed to be maintained without interruption for a huge number of generations to achieve irreversible rewiring of caste-specific developmental pathways for obligate somatic functions (Boomsma, 2009, 2013). In the Hymenoptera, and particularly in the ants, secondary elaborations of superorganismality have included the loss of some, but not all castes (Table 2, qE7), multiple queen mating (polyandry), and re-adoption of newly mated daughter queens back into the nest (polygyny). This underlines that many forms of Wheeler-superorganismality could arise later from a strictly monogamous ancestry and remain evolutionarily stable as long as at least some relatedness was maintained (Boomsma, 2013; Boomsma *et al.*, 2014).

In sum, and slightly modifying Crespi & Yanega (1995), major transitions to superorganismality appear to have three predictable steps: (i) the sequestration of nest-founding 'germ' individuals as specialized breeders, (ii) the allocation of some offspring to somatic functions that imply irreversibly reduced fecundity (e.g. lower termite soldiers; Korb & Heinze, 2016; Korb & Roux, 2012), and (iii) the completion of binary mated/unmated caste differentiation for life among all colony members, marking the evolutionary point of no return where superorganismal coevolution for complementarity between now-permanent caste phenotypes, none of them totipotent any longer, can begin. Only the final step cements reproductive division of labour as an unambiguous

higher-level (full sibling family) adaptation, consistent with how Weismann (1893), Huxley (1930) and Fisher (1930) and later researchers such as Williams & Williams (1957) explained the evolutionary origins of social insect colonies with morphologically distinct castes (Table 2, qE1, qE2, qE4, qS1 and qS8) (see also Owen, 2014).

III. RESOLVING THE TERMINOLOGICAL QUAGMIRE FACILITATES EVOLUTIONARY UNDERSTANDING

(1) Comparing unmated superorganismal castes with sterile organismal soma

As the Page & Mitchell (1993) epigraph at the start of this review indicates, coherence of concepts across the realms of organisms and superorganisms is necessary to understand the stepwise, ratchet-like increases in cellular and colonial complexity from first principles. Life-time monogamy (Boomsma, 2007, 2009) as a necessary condition for any evolutionary origin of eusocial superorganismality (Hughes *et al.*, 2008; Boomsma, 2013) and asexual or single zygote clonality as a necessary condition for any origin of somatic multicellular organismality (Fisher *et al.*, 2013) achieve that coherence (Fig. 3). The fact that parallel processes act across these different domains of social evolution makes sense because a syngamous zygote is an equally strong foundational bond as life-time parental monogamy (e.g. Boomsma, 2007, 2009; Ghiselin, 2011). The life-time commitment principle is consistent with 100% single zygote bottlenecks (Maynard Smith & Szathmáry, 1995) and apparently overrules potential conflicts between co-replicons that may be expressed later in development. For example, plants and animals derived from a single zygote have a nuclear and a cytoplasmic co-replicon whose diverging reproductive allocation interests are normally resolved in favour of the nuclear genes (Cosmides & Tooby, 1981), although cytoplasmic genes in plants occasionally suppress anther formation in flowers, triggering the nuclear genome to evolve compensating modifiers (Leigh, 1977). However, this type of conflict is never relevant before organisms reach sexual maturity, and thus has no bearing on the origins of life-time commitment of two gametes to a single zygote (see Section III.3 for further details).

Moving from diploid plant and animal organisms to diplo-diploid termite superorganisms, the only functional difference is that termite colonies have a tetraploid germ line consisting of the life-time monogamous founding pair (Boomsma, 2009, 2013). However, the default practice of colony founding in haplo-diploid social insects is a triploid analogy (a singly inseminated queen) (Boomsma, 2009), which creates as much inbuilt fraternal conflict as between the egalitarian nuclear and cytoplasmic genes packaged in a plant or animal zygote. This is because hymenopteran stored sperm only passes on genes to daughters and cytoplasmic genes have a similarly exclusive interest in

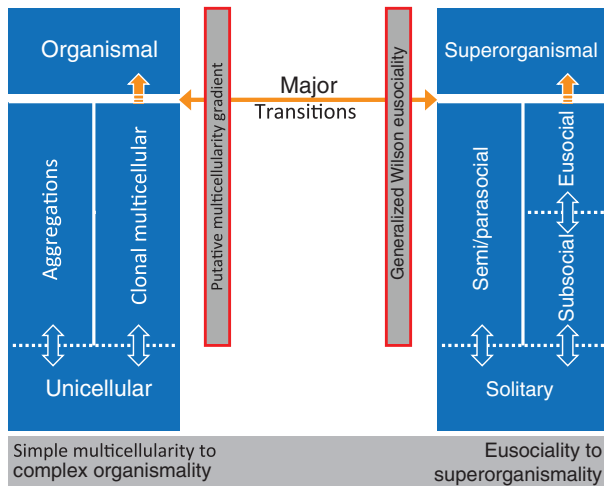


Fig. 3. Parallel major transitions from eusociality to superorganismality in insects and from little differentiated clonal multicellularity to complex organismality in eukaryotes (orange arrows). As shown in Fig. 1 (represented by the right-hand panel here), the semi(para)-social route has allowed obligate breeding in colonies to evolve, but only subsocial and Batra-eusocial ancestors with full-sibling helpers (Table 2, qE8) produced superorganismal lineages *sensu* Wheeler that are universally characterized by physically differentiated queen and worker castes, as in the ants, crown group corbiculate bees, vespine wasps and higher termites (Boomsma, 2007, 2013; Hughes *et al.*, 2008). Likewise (left-hand panel), chimeric aggregation of same-generation cells has only produced simple and temporary forms of multicellularity that normally characterize parts of life cycles or populations, whereas single cell (clonal or zygote) foundation was a necessary condition for the evolution of obligate multicellular organismality (Fisher *et al.*, 2013). As in Fig. 1, double-headed blue arrows indicate transitions that remain reversible. The single-headed orange arrows indicate irreversible transitions, which remain hidden when conceptualizing multicellularity and eusociality as smooth gradients (grey boxes with red frames; see Section III.2).

female reproductive processes. While mitochondrial genes normally remain powerless to increase the proportion of female gametes or offspring, the hymenopteran social insects have an unmated worker caste that does all the brood nursing, and is thus more likely to succeed in pursuing female-biased sex allocation (Trivers & Hare, 1976; Cosmides & Tooby, 1981; Boomsma & Grafen, 1991; Beekman & Ratnieks, 2003). The hymenopteran social insects therefore carry an intrinsic potential conflict load that is absent in the termites (Gardner, Alpedrinha & West, 2012; Alpedrinha, West & Gardner, 2013). However, the fact that Wheeler-superorganismality could evolve in both diploids and haplodiploids demonstrates that these inbuilt conflicts are not decisive for the origins of major evolutionary transitions.

When 100% full-sib colonies are a necessary condition for making transitions from Batra-eusociality to Wheeler-superorganismality, and 100% clonal bodies a necessary condition for making transitions from simple

facultative multicellularity to complex somatic organismality (Fig. 3), the implications are that: (i) aggregative (parasocial) group formation has apparently never produced lineages with universally unmated and morphologically differentiated nursing castes (Fig. 1) (Hughes *et al.*, 2008), and (ii) non-clonal cell aggregations have never produced anything more than very simple cell differentiation when becoming multicellular (Bonner, 1988; Fisher *et al.*, 2013). This logic is not only consistent with Hamilton's rule as outlined in Section II.6, but also with the model by Gardner & Grafen (2009) which concluded that *sensu stricto* superorganismality could never evolve from aggregative processes unless clonality arose as a *deus ex machina* along the way, or some other, presently unimaginable process created zero reproductive conflict. Such characteristics clearly do not apply to lineages that evolved complex organismality or superorganismality (Hughes *et al.*, 2008; Fisher *et al.*, 2013). On closer inspection, these insights also appear to be consistent with a model by Reeve & Hölldobler (2007), where dynamic changes in within-group cooperation and between-group competition were analysed with relatedness within and across groups, group size, and group density as predictor variables. This showed correlated responses for more or less cooperation but without making cooperation go to fixation, i.e. without creating the necessary conditions for the evolution of irreversible group adaptation and obligate physical caste differentiation. In retrospect, it is sobering to realize that Weismann (1893) and Wheeler (1910) captured the essence of exclusive colony-founding bottlenecks *via* queen–male zygote analogues more than a century ago (Table 2, qE1 and qS3), and regrettable that this key insight was subsequently neglected for over half a century.

Table 3 captures the parallels between the evolutionary developments towards superorganismality and multicellular organismality in simple verbal terms, emphasizing the sequential steps towards, and commitment consequences of, irreversible major transitions rather than the changes in key social traits during the origins of new hierarchical levels as shown in Fig. 2. Table 3 is constructed around Bourke's (2011a) insight that social group formation, social group maintenance/elaboration, and social group transformation/transition need to be considered separately (see also Clarke, 2014; West *et al.*, 2015). We use this sequence to evaluate relationships between facultative (plastic) or obligate (morphologically distinct) caste/soma phenotypes (Crespi & Yanega, 1995; Fisher *et al.*, 2013) and the presence/absence of strict life-time founding commitments between two parents or two gametes (Boomsma, 2007). The evidence suggests that there are always two similar precursor states towards a third irreversible major transition state, and supports the conclusion that germ-line sequestration and initiation of unmatedness that we identified at the end of Section II.6 are the final elements of the second step. Only the point of no return completion of these developments, (corresponding to the orange arrows in Fig. 3), appears to depend crucially on precise and lasting relatedness equivalence between offspring and siblings. Systems where this final necessary condition is not 100% fulfilled retain

Table 3. Capturing the transitional routes from solitary breeding to superorganismality and from unicellular eukaryote life to complex multicellular organismality using the scheme by Bourke (2011a), which stipulates that major transitions have three phases of which we postulate that the last one needs to be irreversible: (i) social group formation, (ii), social group maintenance/elaboration, and (iii) social group transformation/transition. Here we combine this sequence with r_o/r_s relatedness-equivalence as a necessary condition for making relatedness terms cancel out of Hamilton's rule, so that major fraternal transitions in hierarchical complexity become possible, but do not necessarily (in fact only very rarely) follow (Boomsma, 2007, 2009). Columns towards the right list key social variables: the necessity or not to breed in colonies or somatic bodies (colony or multicellular life), the necessity or not for the last reproductively totipotent individuals or cells to commit to a life-time nursing caste or soma phenotype (individual commitment), and the ensuing presence/absence of developmental plasticity (phenotypic plasticity for caste/germ line/soma). Step 2 elaborations preceding the irreversible step 3 transitions may include the sequestration of 'germ' individuals or cell lineages and the altruistic specialization of some or even most offspring or cells for somatic functions with reduced fecundity. However, it is the completion of matedness or gametogenesis differentiation for all colony members or cell lineages that defines the points of no return where (super)organismal coevolution between now-permanent caste phenotypes or germ/soma cell lineages can begin. Only this final step 3 has life-time commitment of two founding parents (for social insect colonies) or two gametes (for sexual eukaryotes) as a universal necessary condition. Symbol legend: r_o , relatedness or gene-level reproductive success *via* offspring; r_s , average relatedness or gene-level reproductive success *via* siblings

The route towards superorganismality	Colony life	Individual caste commitment	Phenotypic plasticity for caste
(1) Breeders may or may not have helpers ↓ <i>Cooperative breeding origins</i>	Facultative	Facultative	Present
(2) Breeding only possible in nests with helpers ↓ <i>Eusocial elaborations</i>	Obligate	Facultative or partly obligate	High
(3) All workers remain unmated for life <i>Major transitions to superorganismality possible when</i> $r_s = r_o = 0.5$	Obligate	Obligate	Absent
The route towards complex organismality	Multicellularity	Individual cell commitment	Phenotypic plasticity for germ-line/soma
(1) Unicellular protists may or may not have somatic cells ↓ <i>Aggregations of multicellular protists</i>	Facultative	Facultative	Present
(2) Only multicellular bodies with soma can reproduce ↓ <i>Multicellular elaborations</i>	Obligate	Facultative or partly obligate	High
(3) No somatic cells can enter germ lines any longer <i>Major transitions to complex metazoan organismality possible when</i> $r_s = r_o = 1.0$	Obligate	Obligate	Absent

at least some of their phenotypically plastic (behavioural) helper phenotypes, or relatively undifferentiated somatic cell phenotypes. Only 100% relatedness equivalence removes any form of preference for direct or indirect fitness benefits in families of cells or siblings, underlining the fact that major transitions to organismality and superorganismality are convergent phenomena. It is only at these major transitional points that reproductive altruism by cell copies or offspring becomes mostly unconditional through the irreversible loss of reproductive totipotency in gametogenesis and matedness. After such major fraternal transitions are completed, occasional selfish traits are expressed only by some individuals (e.g. Woyciechowski & Kuszewska, 2012) or cell lineages (e.g. Buss, 1987), and usually under a narrow range of conditions.

(2) Identifying major transitions with continuous gradient concepts is difficult

Before we proceed to evaluate some of the wider implications of our analyses, it is appropriate to mention alternative approaches that have been used to characterize transitions

to (super)organismality and their correlates. First, Michod (2000), Folse & Roughgarden (2010) and Bourke (2011a) have followed Buss (1987) and Huxley (1912) in using the term 'individuality' instead of 'organismality'. While this terminology can be useful, the idea that a social group of cells or animals can be considered more or less of an individual appears to be connected to the assumption that major transitions can happen *via* aggregative (parasocial) pathways of 'coming together'. This overtly anthropomorphic view goes back to Henry Ford's well-known remark that 'coming together is a beginning, keeping together is progress, working together is success'. This sequence captures some of the variation in social cohesion across facultative multicellular lineages or along cooperative breeding and facultative eusociality gradients (left of the orange bar in Fig. 2), but fails to recognize that the dichotomous point of no return that defines any subsequent major transition could only happen *via* the subsocial route, where maximal relatedness is a necessary condition for 'keeping together' and where 'coming together' is represented only by parental life-time commitment (Fig. 3). In contrast to terminology based

on (super)organismality, individuality language does not naturally invite asking what the necessary and sufficient conditions for major transitions are, and neither does it allow the insight that ratchet-like major transitions represent the only unambiguous examples of matter-of-fact progress in evolution. Using the top-down (core family based) life-time commitment principle for explaining the origins of major fraternal transitions thus clarifies the underlying evolutionary processes that are missed when using a levels-of-selection perspective based on bottom-up coming together of same-generation units (Pepper & Herron, 2008; Clarke, 2011, 2014; Okasha, Weymark & Bossert, 2014; Okasha, 2015). As our analyses indicate, bottom-up coming together completely lacks the prospect of ever realizing a major fraternal evolutionary transition.

Second, intra-colony conflict levels tend to decrease with colony size (Bourke, 1999), both when colonies have behavioural castes and when they have morphological castes, but the type and impact of conflict between lineages with and without morphological caste differentiation is fundamentally different. Pre-superorganismal conflict reduction (top-left section of Fig. 2; step 2 in Table 3) is primarily about direct fitness and reproductive skew between individuals whose mating totipotency is intact (e.g. Strassmann *et al.*, 2002; Nonacs & Hager, 2011), whereas conflict reduction in superorganisms (top-right section of Fig. 2, i.e. after the irreversible step 3 in Table 3 has been completed) is mainly about allocating resources to reproductive brood with maximal indirect fitness returns to make the best of permanent worker-caste fate. Irreversible loss of reproductive totipotency is therefore itself a key conflict-resolving mechanism. The main reason for superorganismal colonies reaching larger size (Bourke, 1999) thus appears to be that life-time unmatedness of workers avoids reproductive skew conflicts, altogether in higher termites, and (usually) as long as the queen is alive and fertile in the haplodiploid social Hymenoptera. When superorganisms became perennial from short-lived ancestral states comparable to extant bumblebees and vespine wasps (Fig. 2), policing and coercion were typically further elaborated as conflict-regulating mechanisms, but mostly as secondary elaborations in response to lower offspring relatedness when colonies started to adopt or replace queens, or queens evolved multiple mating (Hammond & Keller, 2004; Ratnieks *et al.*, 2006; Ratnieks & Helanterä, 2009; Woyciechowski & Kuszewska, 2012; Boomsma *et al.*, 2014) (but see Zanette *et al.*, 2012). This implies that colony size is unlikely to be a universal driver of social evolution, but an important correlate with different causes and consequences on either side of the orange bar in Fig. 2. Because of these differences, median colony size in Wheeler-superorganisms (right side of Fig. 2) is much larger than in cooperative breeders and eusocial lineages without life-time castes (left side of Fig. 2), but the ranges overlap as some superorganismal colonies have remained or become very small and swarm-founding paper wasp colonies can be very large. Such overlap is all but absent in comparisons between aggregative facultative multicellularity with minor

differentiation in cell types and zygote-founded organismality with complex soma (Bonner, 1988), e.g. slime mould slugs *versus* the smallest bilaterian metazoans, to say nothing of elephants or whales.

Third, Queller & Strassmann (2009) and Strassmann & Queller (2010) have used organismality terminology, but retained a sociobiological continuum approach in their analyses of cooperation and conflict gradients, which we believe is unsatisfactory because it continues to lump (*cf.* Wilson, 1975; Sherman *et al.*, 1995) distinct domains of complexity that are separated by major evolutionary transitions. Not acknowledging the fundamental importance of permanent castes and permanent soma means one cannot be explicit either about the causes of secondary elaborations on either side of such transitions being distinct. For example, differences in social organization between colonies of *Polistes* and *Polybia* wasps (Jeanne, 1991; Strassmann *et al.*, 2002) (both lacking distinct permanent adult caste phenotypes for most if not all colony members) are functionally non-homologous with differences between bumblebees and stingless bees (Kapheim *et al.*, 2015) (both having made the transition to superorganismality, such that all individuals are either mated or unmated for life). In both cases, the more elaborate social system evolved dispersal by swarming to reduce colony-founding mortality, and both shifts coincided with transitions from annual semelparity to perennial iteroparous breeding with much larger colonies. However, dominance hierarchies became more carefully regulated in the perennial polistine wasps, while the perennial bees achieved conflict reduction through the more elaborate domestication of a single queen by life-time unmated workers (Bourke, 1994; Boomsma *et al.*, 2014; see also Loope, 2015 for an analogous case in vespine wasps). All colony members belonging to a single physically differentiated caste for life changes everything, as does the emergence of animal soma that is irreversibly differentiated from the germ cell lineage. This was perfectly transparent to naturalists before sociobiology took off, as emerges from Williams's (1966) seminal monograph *Adaptation and Natural Selection*, from a book review by Hamilton (1967), and a host of earlier contributions (Huxley, 1912, 1930; Fisher, 1930; Lüscher, 1953) (Table 2, qE4, qS5, qS8 and qS11).

(3) Initial adaptations to higher levels of hierarchical complexity are about synergistic resource acquisition, not reproductive harmony

The co-replicons of complex multicellular organisms (autosomes, sex chromosomes, and maternally transmitted cytoplasmic elements) (Cosmides & Tooby, 1981) have fundamental resource allocation conflicts about sex, sex ratio, and social behaviour, but never about mechanisms of resource acquisition, infrastructure maintenance, and immune defence. In the same way, caste-differentiated superorganisms lack cross-purpose conflict for higher-level somatic functions (Ratnieks & Reeve, 1992; Queller & Strassmann, 2002; Boomsma & Franks, 2006). Traits for optimizing foraging, nest building, communication, and

social disease control are therefore free to evolve as complex ‘somatic’ colony-level adaptations that are heritable and selected at the colony level only (Bonabeau *et al.*, 1997), a fact already envisaged by Huxley (1912, 1930), Weismann (1893), Wheeler (1910, 1923, 1928b) and others (e.g. Table 2, qE1–2, qE4, qS1, qS3, qS5, qS7). However, this is highly unlikely to happen in facultatively eusocial dominance hierarchies *sensu* Crespi & Yanega (1995) (e.g. Table 2, qS17) where – in spite of colony-life being obligate (Table 3) – foragers often provision larvae themselves and genetic heterogeneity within nests will maintain selection for at least some individual discrimination according to degree of kin (Strassmann *et al.*, 2002), a process that is generally absent in superorganisms (Boomsma & d’Ettorre, 2013).

The key significance of separation between resource acquisition and resource allocation appears to apply in similar measure when considering adaptive functions of unicellular cell division *versus* germ-line reproduction aided by complex soma. The Metazoa did not become organismal in the complex unitary soma sense until the origin of the mesoderm (gastrulation), which separated mouth and gonads (i.e. resource acquisition and reproductive allocation) during development and simultaneously cemented unambiguous germ line sequestration (Barfield *et al.*, 2016). By contrast, although the prokaryotes and protists may express forms of simple multicellularity (Fisher *et al.*, 2013), they continue to experience resource acquisition conflicts over public good investments, as a plethora of studies have documented (Diggle *et al.*, 2007; Cordero *et al.*, 2012; Dumas & Kummerli, 2012; Oliveira, Niehus & Foster, 2014; Andersen *et al.*, 2015; Rendueles *et al.*, 2015). As it appears, conflicts over resource acquisition are ubiquitous as long as all or most cell divisions are reproductive rather than somatic events. Crucially, however, these conflicts disappear after multicellularity has become obligate with unambiguously sequestered germ tissues and differentiated soma of maximal relatedness. This is consistent with complex organismal plants and animals always needing a period of pure somatic growth before they can reach sexual maturity, in the same way as Wheeler-superorganisms need an ergonomic phase of pure worker production (Oster & Wilson, 1978) before colonies can rear dispersing reproductives. Thus, neither complex multicellular organisms, nor Wheeler-superorganisms appear to experience any allocation conflict that might interfere with growth until they are sexually mature, and even then the expression of conflict will not compromise (super)organismal coherence (Table 2, qS2 and qS11).

We have no space here to review all the empirical evidence, but there appears to be considerable support for superorganismal colony-level adaptations never being associated with reproductive allocation. Typical examples of such adaptations have been discussed by Seeley (1989, 2010), Hölldobler & Wilson (2009), Ratnieks & Reeve (1992), and others. The following offers a reasonable summary: (i) honeybee dance language for efficient foraging (Dyer, 2002), (ii) nest-building and foraging routines, including the complex

communication mechanisms involved (Bonabeau *et al.*, 1997; Duarte *et al.*, 2011), (iii) thermoregulation and other forms of active nest environment control (Hansell, 1993), (iv) additional morphological differentiation of helpers when evolutionarily derived soldier castes or additional nursing castes evolve (Wilson, 1971), and (v) social immunity strategies (Cremer & Sixt, 2009; Tragust *et al.*, 2013). All these examples concern optimization of resource acquisition, infrastructure maintenance, public health measures and somatic defence, and none have any bearing on how or when potential reproductive conflicts may be expressed or regulated. If this reasoning is correct it might be possible to develop a formal reproductive value calculus for Wheeler-superorganisms, to complement the derivation of a Fisherian fundamental theorem of multilevel natural selection (Gardner, 2015).

(4) Precise terminology matters because misnomers breed misunderstanding

It was not until the mid-18th century that Linnaeus unambiguously categorized the whales as mammals rather than fishes. This insight was based on the recognition that all mammals have lungs, warm blood, hair, and produce live-born offspring that are milk fed (Romero, 2012). It pre-dates Darwin’s evolutionary assessment of whales representing a secondary return to marine life by a century. Today, nobody would question the validity of this taxonomic split that had been staring naturalists in the face since the time of Aristotle; aquatic mammals and fish are two very different things. The sociobiology program (Wilson, 1975) was built upon a heuristic narrative that obscured equally significant splits in functional taxonomy, using a lumping approach to force-fit obviously different stages of social evolution under ‘swimming in the water’ umbrellas called ‘eusociality’ and *sensu lato* superorganismality. These concepts are neither valid taxonomic categories, nor useful research tools, but arbitrary human constructs. As it appears, key elements of what some (e.g. Nowak, Tarnita & Wilson, 2010) conceive as a controversy over the validity of inclusive fitness theory (for responses see Abbot *et al.*, 2011; Boomsma *et al.*, 2011; Bourke, 2011b; Ferriere & Michod, 2011; Herre & Wcislo, 2011; Strassmann *et al.*, 2011) emanate from the fact that Wilson’s (1971) broad definition of eusociality (Table 2, qE15) glosses over the major transitions to superorganismality as defined by Wheeler (1911) (Fig. 1).

Against such a misnomer background, it is often impossible to assess what the phrase ‘the evolution of eusociality’ actually means. It may be about the very first offspring adopting a helper role, about discrete defensible nests or colonies, about castes differing only in behaviour, about physically differentiated castes, about colonies having a few offspring with a distinct soldier phenotype, or about an even less specified form of *sensu lato* superorganismality. As the inventor of the term eusociality (Batra, 1995) highlights (Table 2, qE8, qE14 and qE19), almost anything social can be made to fit the three sociobiology criteria for eusociality – cooperative brood care, reproductive division of labour and generation overlap (see McAuliffe & Whitehead, 2005, for a recent

example). Papers emerging from this approach often use all of the aforementioned interpretations of eusociality interchangeably (e.g. Nowak *et al.*, 2010), which illustrates that the sociobiology definition of eusociality is a meaningless panchestron. This term, used by Hardin (1956) to argue that the concept of protoplasm needed to be abandoned because it was empty of content, was also applied to dismiss the Wheeler-superorganism (Table 2, qS12) in the 1960s. This is somewhat ironic because Wheeler-superorganismality is a well-defined concept, whereas sociobiological eusociality continues to be pushed in increasingly meaningless directions (Table 2, qE23). It would, in fact, not be unreasonable to conclude that the three-part sociobiological definition of eusociality which originated in the 1970s has become the protoplasm of 21st century social evolutionary theory.

The catch-all eusociality definition and its *sensu lato* superorganismality companion have even allowed the suggestion that humans are also 'eusocial' (Nowak *et al.*, 2010; Wilson, 2012). The only reference to support this claim is an out-of-context mention of a note by Foster & Ratnieks (2005) suggesting that human menopause is an obligate altruistic trait. However, their argument has no bearing on reproductive division of labour or breeding status across women, because there is no obvious relationship between life-time reproductive success and age at menopause, not to mention the fact that human queens are as menopausal as normal female citizens. Before we even entertain the possibility of humans matching ants and termites by some loose analogy, it is important to make explicit that the universal loss of reproductive totipotency in these social insects almost always implies life-time commitment of every colony member to a single core or extended family and extreme mutual dependency, points elegantly driven home by Weismann (1893), Wheeler (1902, 1910), Fisher (1930), and others (Table 2, qS1–3, qS8 and qS11). While such obligate dependency may be every dictator's dream, it is neither a realistic nor a desirable model for human society. Neither do modern humans have the required monogamous ancestry; we are rather monogamous compared to our great-ape sister lineages (Kramer & Russell, 2015), but nothing that comes even close to the life-time monogamy of the ancestors of superorganismal social insects (Boomsma, 2007, 2009; Hughes *et al.*, 2008). Writing on this issue Huxley (1930) captured in a few well-chosen sentences how misleading it can be for researchers to draw parallels hastily between insect colonies and human societies (Table 2, qS9), echoing that Wheeler was right and Spencer was wrong about the organisms that have evolved superorganismality (Table 1).

In retrospect, it is surprising how unsuitable the sociobiological 'just so' definitions of eusociality and *sensu lato* superorganismality are for obtaining insight into the fundamentals of social evolution. This contrast is particularly striking when reflecting on the crystal-clear logic of many leading authors who wrote about social insects before sociobiology took off. For example, Weismann (1893) offered an eloquent 30-page verbal summary of ant biology that we

can hardly do justice to with the three quotations included (Table 2, qE1, qE2 and qS1). Among other things, he explained: (i) how families consisting of a single inseminated queen and her offspring respond to family-level selection with maximal efficiency; (ii) the factors that impose positive and relaxed selection on ant colonies; (iii) how co-adaptation between complementary caste phenotypes is maintained even when social parasites usurp colonies; (iv) the significance of worker reproduction and old queens running out of sperm; and (v) the factors that promote division of labour and the secondary evolution of soldier castes. Much of this scholarship was cited or reiterated by Wheeler (1910, 1911, 1923, 1928b) and Huxley (1912, 1930), so it is puzzling that many of these insights remained unreported when *The Insect Societies* (Wilson, 1971) and *Sociobiology* (Wilson, 1975) appeared in the 1970s.

The concept of family selection for maximal fertility that Weismann, Huxley, Wheeler and Fisher used to explain the evolution and maintenance of physically differentiated castes (Owen, 2014) (Table 2, qE1–qE4, qS1, qS3 and qS8) was an elaboration of Darwin's (1859) explanation for the evolution of sterile castes in insect colonies. After Darwinian adaptationist logic and Mendelian genetics had been synthesized, both Haldane (1932, p. 120) and Sturtevant (1938) concurred with Fisher's assessment of family selection, showing that all three of these leading geneticists were very explicit in their understanding of permanent reproductively altruistic castes as the product of selection on genetically closed families (Table 2, qE5, qE6 and qS8). Although these statements are consistent with the life-time commitment principle at colony founding, these early authors also implicitly assumed, as Darwin must have done (*cf.* Kirby & Spence, 1818), that all social insect queens are singly inseminated, because multiple mating in the honeybee was first documented about a decade later (Roberts, 1944). However, when scrutinizing these quotes, their logic never appears to depend critically on maximal offspring relatedness being maintained after superorganismality evolved, so multiple queen mating appears to have become a distraction until it was realized that, at least in its obligate form, it is an evolutionarily derived superorganismal trait (Boomsma, 2007, 2009, 2013; Hughes *et al.*, 2008). Also the pioneering study by Williams & Williams (1957) is based on this closed family principle. To summarize, it can hardly be emphasized enough how fundamentally different family selection is from group selection. As explained in Section III.2, groups are bottom-up social structures. They come together as chimeric aggregations or parasocial assemblies that are incapable of forging major evolutionary transitions, whereas families are top-down 'staying together' pedigrees, which have the potential to transition to new, higher organizational levels, albeit under a series of very specific, unlikely, and onerous conditions (Fig. 3) (see also Boomsma, 2016).

The authors of many social insect papers published since the 1970s have used Wilsonian eusociality terminology, assuming that it represented some form, and often the highest form, of social organization without worrying about the

validity of definitions. The first author of this review has been among them since the 1980s, using the term eusocial when referring to social insects (usually ants) with physically differentiated castes, but then becoming gradually aware that there are fundamental problems with the catch-all oversimplified definition of eusociality. As we show here, Weismann (1893), Fisher (1930), Haldane (1932), and Hamilton (1964*b*, 1967) all contributed erudite interpretations of selection on life-time committed parents for ergonomic efficiency in family-based colonies with reproductive and sterile castes. These accounts either inspired or followed Wheeler (1910, 1923) (Table 2, qE1, qE2, qE4, qS1 and qS8) but, as mentioned earlier, almost none of this can be retrieved from the monographs that established sociobiology (Wilson, 1971, 1975). In its zeal to turn ants into model systems for understanding social evolution elsewhere, the sociobiology tradition has tried to make us believe that we can ignore fundamental natural history for the sake of shallow comparative analogy. It is well known that early critics maintained that the sociobiology approach was founded on ‘just so’ stories (Segerstråle, 2000). As far as that critique had merit it has now largely been remedied by solid hypothesis-driven approaches in the well-established field of behavioural and evolutionary ecology (e.g. Krebs & Davies, 1978, 1984, 1991, 1997; Trivers, 1985; Cockburn, 1991; Davies, Krebs & West, 2012) of which sociobiology became part (Table 1). However, our present analysis exposes that, for the social insects, the sociobiology research program was originally based on unfounded ‘just so’ definitions and arbitrary classification systems, which represents a more fundamental problem that we here attempt to resolve.

(5) Where to go from here

As we stated in Section I, there are scientific contexts where the precision of eusociality and superorganismality terminology does not matter greatly, but it is almost invariably illuminating to acknowledge Wheeler’s physical caste criteria for superorganismality, which entails that all superorganismal colonies had sub-social and Batra-eusocial ancestors. Huxley (1930) concisely summarized that there are three main grades of insect social organization: (i) a lower subsocial family grade with parental care only, (ii) a middle ‘true social, or colony, grade’ in which adult offspring cooperate with parents in colonial nest building and caring for younger siblings, and (iii) a highest caste-based grade consisting of a fertile reproductive caste and ‘unsexed neuters’ doing all other tasks (see Table 2, qE4 for the original formulation). Huxley’s (1930) ‘true social, or colony, grade’ of organization (Table 1) is the same as Batra’s (1966*a*) eusociality, and his entire scheme is almost identical to ours in the upper part of Table 3. The highest caste-grade identified by Huxley (1930) corresponds functionally with Wheeler’s superorganism, which explains why he cites Wheeler’s insights approvingly throughout his early career (Huxley, 1912, 1930). All other social systems are then best referred to as forms of cooperative breeding (Crespi & Yanega, 1995)(Fig. 2).

Acknowledging that the origins of superorganismality rely on universal life-time monogamy and full-sibling family life makes it explicitly clear that the term superorganism is inapplicable to vertebrates, which are never monogamous enough (Boomsma, 2013), and that it should not be applied to seemingly harmonious open assemblages that violate the co-replicon principle (Cosmides & Tooby, 1981). Representative examples of untenable superorganism terminology of the latter kind (Table 2, qN1–qN7) illustrate how essential it is to have precise and correctly targeted definitions if we are to understand why some social insect lineages passed the point of no return to superorganismality, while other social clades of arthropods and vertebrates did not (Figs 1 and 2; Table 3). Much precision would also be gained if biologists would be explicit on whether they address origins of superorganismality *sensu* Wheeler (1911) based on physically differentiated castes, or secondary (evolutionarily derived and elaborated) superorganismality as identified by Seeley (1989). However, the Wilsonian *sensu lato* version of the superorganism (Hölldobler & Wilson, 2009)(Table 2, qS22 and qS24) needs to be abandoned. That terminology has confused specialists and non-specialists alike, has no foundation in Darwinian principles (Weismann, 1893; Wheeler, 1911, 1923; Fisher, 1930), and no obvious connection to the major transitions framework (Maynard Smith & Szathmáry, 1995).

As for eusociality, that term is now so entrenched that there is no feasible way to restrict its use to small monomorphic insect families, as Huxley (1930) and Batra (1966*a*) originally intended with their essentially identical versions of ‘true sociality’ (Table 2, qE4, qE8). However, qualifying the term with the facultative and obligate designations proposed by Crespi & Yanega (1995) (Fig. 1) goes a long way towards resolving the problem of having a system for the classification of social behaviour that is both practical and biologically meaningful. The adjusted terminology would be useful because: (i) the identification of systems with and without physically differentiated reproductives and workers is almost always straightforward; (ii) the corresponding facultative–obligate eusociality terminology captures that there is a fundamental difference between the cooperative breeding gradient ending with facultative caste commitment for most colony members and the more advanced Wheeler-superorganisms (Fig. 2). The former are societies whose members form reproductive dominance hierarchies as organisms but remain, as gene pools, uncommitted to superorganismality. In the latter all colony members have specialized caste phenotypes for life. Here colonies are no longer societies because no member has retained fully independent ‘agency’, and it is therefore here that unconditional adaptations to higher-level somatic functions have evolved.

When used properly, inclusive fitness arguments never aim to explain the origin of artificial behavioural categories, or any other classifications we impose on the natural world. Instead, they make testable predictions about how and why specific traits such as altruistic behaviour or

physically differentiated caste phenotypes have evolved (Queller, 1996; Abbot *et al.*, 2011). Sometime in the early 1980s, the fundamental distinction between trying to explain key social traits rather than an artificially lumped behavioural classification became opaque when some mistakenly began to treat Wilsonian eusociality as a trait. Soon after it became a research agenda to explain the evolution of this reified category that no one could define in terms that clearly set it apart from any other social category (*cf.* Batra, 1995; see also Table 2, qE14 and qE19). An important insight to emerge from our analysis is that the commonly asked question, ‘What explains the evolution of eusociality?’ is malformed, and has no meaningful scientific answer. Without further qualification, the term is unsuitable for use in the pursuit of a first-principles understanding of social evolution because unspecified eusociality cannot respond to any form of natural selection.

Reinstating coherent definitions, and making them practically applicable to basic research will benefit the study of social evolution in multiple ways. Hamilton’s rule applies across the domains of social evolution, and also to the fraternal transitions between them during which relatedness terms cancel out. Yet, the key social traits to be explained differ fundamentally between the cooperative breeding and non-caste-committed eusociality domain on the one hand, and the Wheeler-superorganismal domain on the other (Fig. 2). This implies that colonies with permanent, morphologically differentiated castes are as distinct from those with behavioural ‘castes’ as bilaterian metazoans are from *Dictyostelium* slime moulds.

IV. CONCLUSIONS

(1) We have analysed more than a century of scholarly thinking about superorganismality, and conclude that the modern versions of the superorganism which arose in the 1980s lack conceptual coherence compared to the original version that Wheeler (1911) proposed.

(2) We explain that the root cause of these flaws is the generalized definition of eusociality that came into fashion when sociobiology took off in the 1970s. This definition merely emphasized loose similarities in cooperative brood care, reproductive division of labour and generational overlap, thereby lumping all social breeders together in a single convenience category while ignoring the key significance of the presence or absence of permanent, physically differentiated queen and worker castes.

(3) We document that early naturalists such as Darwin, Weismann and Wheeler had a very straightforward family-selection understanding of social evolution in genetically closed insect colonies that was accepted by Fisher, Haldane and Huxley in the 1930s, but disappeared from the literature in the 1960s, becoming an intellectual fossil deposit that we recover in this review.

(4) We combine these early insights with recent developments of inclusive fitness theory and the major

evolutionary transitions paradigm to show that Hamilton’s rule is sufficient to identify the only known necessary condition for all irreversible fraternal eukaryote transitions to complex multicellular organismality and caste-differentiated superorganismality: life-time commitment by two gametes in a single organism-founding zygote or a strictly monogamous royal pair founding an insect colony, i.e. 100% diploid single-cell bottlenecks, or its triploid/tetraploid analogy in founding royal pairs of social insect colonies.

(5) We argue that gradual conflict reduction in chimeric same-generation social aggregations of cells or organisms has never produced a major transition in evolution, and cannot be expected to do so either. Both conceptual logic and comparative data show that such transitions always require parent-offspring associations with maximal average sibling relatedness – mathematically identical to parental relatedness to offspring – so that the relatedness terms to offspring and siblings cancel out of Hamilton’s rule. In other words, major transitions in evolution require relatedness equivalence first and benefit–cost facilitation afterwards, not the other way around.

(6) In this view, major transitions are simple mathematical singularities during which offspring relatedness is both universally maximal and not differentiable (Boomsma, 2007). Life-time foundation commitments thus imply that major transitions in evolution do not originate via a dynamic process of kin-selection because there is no variation in relatedness when it is always maximal. However, before and after such irreversible transitions, all three parameters in Hamilton’s rule vary simultaneously and without priority for either relatedness or costs/benefits of reproductive altruism. This implies that social evolution by kin selection always follows the logic of Hamilton’s rule, but that the outcomes are fundamentally different in the organismal and superorganismal domains of social evolution.

(7) We show that the presence of potential reproductive conflict cannot prevent major transitions to complex (super)organismality as long as the life-time-commitment founding principle is upheld as a necessary condition, and the benefit–cost difference of unconditional altruism is positive and uninterrupted for the many generations needed for selection to split developmental pathways into irreversibly differentiated germ and soma functions. This is because reproductive conflicts in multicellular organisms and superorganismal colonies are not about joint resource acquisition (which provides the key synergy benefits), but about reproductive resource allocation after, not before reaching sexual maturity.

(8) We argue that recurrent controversies about the validity of inclusive fitness theory are, in large part, a result of the poorly defined sociobiological concepts of eusociality and superorganismality. Because the sociobiological definition of eusociality is merely a loose human construct that emphasizes shallow similarities rather than distinct quantifiable traits, it is meaningless to ask without further qualification how such a category evolves. We propose a few simple adjustments in terminology that will go a long way toward resolving

these conceptual issues that have been a hindrance to understanding social evolution from first principles.

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